STRUCTURE, FUNCTION, AND STABILITY OF INTERCROPPING SYSTEMS IN TANZANIA

BY

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STRUCTURE, FUNCTION, AND STABILITY
OF INTERCROPPING SYSTEMS IN TANZANIA

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Effects of crop diversity on system productivity and stability formed the subject of a two-year study of nine Tanzanian cropping systems and successional vegetation. Planting density was controlled so that intercrop-monoculture differences were due solely to diversity, not density, effects.

Various measures of seasonal biomass accretion were used as indicators of net productivity. The ordering of systems by productivity, from high to low, was successional vegetation, maize-sorghum, maize-pumpkin, sorghum, maize-sorghum-cowpea-pumpkin, sparse maize, recommended density maize, maize-cowpea, cowpea, and pumpkin. Intercrop performance was compared with that of a mixture of corresponding monocultures by Yield Equivalent Ratio (YER), a new index defined as the ratio of yield in intercrop to expected yield based on planting densities and monoculture yields. By this measure, intercrops were more productive than corresponding monocultures, but the advantage was lowest under a 50 percent defoliation treatment. Species YERs were greater than one for maize, sorghum, and cowpea, and less than one for pumpkin.

The productivity advantage of diverse systems was due primarily to a greater amount and a more even distribution of leaves and roots, temporal partitioning of growth, complementary resource response curves, and compensatory growth. Several of the 23 pests and diseases inventoried were correlated with crop yield, but few were significantly more or less abundant in intercrops than monocultures. Efficiency of labor use in intercrops was equal to or greater than that in monocultures.

The ordering of systems by yield stability (constancy), from high to low, was sorghum, maize, succession, four-crop intercrop, cowpea, and pumpkin. Intercrop stability was higher than that of component crops grown as monocultures. Yield of sorghum, cowpea, and pumpkin, but not maize, was less stable in intercrops than monocultures; decreased species stability in diverse systems may enhance system stability through compensatory growth. Stability was greatest under low levels of stress.

CHAPTER ONE
INTRODUCTION

Parallel lines of research in the agronomic and ecological sciences have focused on the effects of vegetation diversity on ecosystem productivity and stability. The agronomic approach has consisted mostly of experimental studies of various crop combinations, with relatively little attention (until recently) to the causes of differences in yield, and considerable confusion over the indices used to compare the performance of diverse and simple systems. Comparisons of systems of unlike density have further confused the issue. The ecological approach has emphasized theoretical mechanisms underlying the diversity-stability relationship, mathematical models of competition and resource partitioning, computer simulation of diverse and simple systems, and broad comparative ecosystem studies, with relatively few controlled experimental studies. In this study I integrate these two approaches by using agronomic systems to conduct a controlled experiment testing the effects of diversity on various aspects of ecosystem structure and function. The experimental design allows conclusions to be made regarding the effects of spatial diversity, not confounded by varying species composition and planting density.

The Ecological Issues

Diversity, Stability, and Competition

The question of whether increasing species diversity increases stability, and the relationship of diversity and stability to productivity, have been recurrent issues in the ecological literature for many years. Several volumes have been devoted to these topics, drawing on evidence ranging from global latitudinal comparisons to laboratory microcosm experiments, mathematical models, and computer simulations (Woodwell and Smith 1969, May 1973, Pielou 1975, van Dobben and Lowe-McConnell 1975), van Voris 1976). The issue is still far from being resolved, but Goodman (1975) and Murdoch (1975) concluded that although species diversity *per se* is not a good predictor of stability (especially in agricultural and model systems), certain correlates of diversity may be causally related to stability.

Current literature tends to substitute more specific, mechanistic hypotheses for the generalized diversity-stability question. A large increase in entomological studies, for example, has begun to elucidate the roles of resource concentration, pest dilution, feedbacks between trophic levels, time lags, search behavior, microclimate, and natural enemy dynamics on pest levels, pest stability, and various methods of pest control in diverse and simple systems (reviewed by de Loach 1970, Southwood and Way 1970, Hassell and May 1973, Comins and Blatt 1974, Huffaker 1974, van Emden and Williams 1974, Barclay and van den Driessche 1975, Murdoch 1975, Murdoch and Oaten 1975, Shattock 1976, Trenbath 1976, Way 1976, van Emden 1977, Levins and Wilson 1980). No clear conclusions can be drawn on theoretical grounds regarding the effects

of diversity on pests; there are many mechanisms that may stabilize and reduce pest levels in simple systems as well as complex systems. Perhaps the best way to summarize the theoretical effect of plant diversity on pest levels and pest stability is that it is unpredictable due to the complexity of interactions involved.

There has also been a resurgence of interest in competition reduction through resource partitioning as a mechanism that may increase productivity and stability in diverse systems (reviewed by Pianka 1981). May (1981) and Nunney (1980) modeled growth rates of two interacting populations using Lotka-Volterra competition equations. Pianka (1981) noted, however, that while these models are useful, they greatly oversimplify the competitive mechanisms involved among species. It is also likely that the competition coefficients in these equations vary with growing conditions and planting diversity (Vandermeer 1981).

The theory of niche separation was presented by Pianka (1981), and biological mechanisms of resource partitioning were reviewed by Schoener (1974). Increased light use efficiency in canopies composed of sun- and shade-adapted species was discussed by Donald (1961), Black (1975), and Boardman (1977). Bray (1974) noted that root competition for nitrogen and water can occur at low root densities due to those substances' high mobility in soil, and Litav and Wolovitch (1971), Parrish and Bazzaz (1976) and Berendse (1979) discussed the temporal and spatial separation of root zones. Partitioning of nutrient element demand was suggested by the results of Garten (1978), who showed that concentrations of elements in plant tissue may vary from species to species at a site.

The question of whether natural successional regrowth constitutes the most effective possible use of resources at a site has not been completely resolved. It may not be, at least in the short term; pastures and sugar cane are two examples of human-managed systems composed of a few highly productive species that may produce more biomass on a site than succession (Odum 1971, Mott and Popenoe 1977). Whether, and by what biological mechanisms, the productivity and stability of successional systems can be improved upon is still an open question.

Definitional Problems

The definitions of diversity and stability have been a source of confusion. Hurlbert (1971) reviewed the various diversity indices in use and concludes that they are not necessarily correlated, cannot be shown to be useful measures of a meaningful community property, and should be replaced by other measures of ecosystem characteristics more appropriate to the specific issue at hand. Stability is an even more confused concept; its meaning includes properties of constancy (both absolute and in relation to the mean), predictability, resistance, and resilience (Holling 1973, Goodman 1975, Murdoch 1975 and Orians 1975). The most commonly used measures of species constancy are coefficient of variation (e.g., Rao and Willey 1980 and other studies cited in Trenbath 1974), and standard error of population levels or changes (Watt 1965). Other measures of stability, less commonly used, relate to degree and rate of response to perturbations (Orians 1975).

Constancy on the community level could be measured as coefficient of variation or standard error of system attributes such as total productivity or leaf area, rather than as population counts; Murdoch et al. (1972) evaluated insect community stability with a similarity index of two years' sweep net samples. Margalef (1969) proposed a community stability index that is the sum of the quantity (biomass·biomass half-life) for component species. Other measures of community stability with respect to perturbations have been suggested by Orians (1975).

Stress and its Relation to Productivity and Stability

The general definition of stress by Odum (1967) as diversion of potential energy in response to a stressor is robust, and will be used in this study in preference to that of Grime (1979), who limited the term to chronic low-productivity conditions and excluded other possible energy drains such as competition or disturbance. Lugo (1978) pointed to the type of stressor, its duration (chronic vs. acute), point of impingement, and degree of system adaptation as factors that will determine the rate and degree of system response to stressors. Rapport (1981) differentiated between "alarm" reactions in non-preadapted systems and "coping" reactions in resistant, preadapted systems (an analogy with human response to disease). Stress can be measured as decreased productivity, increased energy drains, or acceleration of repair within the system (Odum 1967). Stressors, like limiting factors, are thought to interact multiplicatively, rather than additively, with respect to productivity (Odum 1971, Lugo 1978).

If we accept the definitions of stress as reduced productivity, and stability as low fluctuation in productivity, a link between the two concepts becomes apparent. Stability can be viewed as a system's ability to adjust to varying intensities of stressors to maintain productivity at a constant level. Degree of preadaptation will largely determine the stability of the system with respect to a stressor (as was pointed out, in the context of pest populations, by Huffaker 1974, Goodman 1975, and Murdoch 1975). If stressors do interact multiplicatively, then reduced intensity of some stressors (such as competition or herbivore drains) should reduce the magnitude of productivity response to other stressors. If diverse systems are more productive than simple ones due to resource partitioning, reduced drains, or other factors, it would not, then, be surprising to find that they are also more stable than simple systems.

Environmental parameters such as level, constancy, and predictability of limiting factors, describe the setting in which stabilizing biological adjustment occurs. Such parameters may be critical in determining ecosystem productivity and stability across a range of environments (Zaret 1982). Environmental effects may also explain the noncorrelation of productivity and stability in (high-productivity, low-stability) marsh and pond ecosystems, and (low-productivity, high-stability) paramo vegetation and marine benthos systems. It is within a given environment that the biological mechanisms leading to system stability can best be explored, since differences in system behavior due to differences in environmental parameters are controlled.

The Agronomic Issues

Green Revolution technology assumed abundant supplies of fossil-fuel energy at affordable prices. Dramatic increases in the cost of energy inputs to agriculture (mechanization, improved seed, fertilization, pesticide, irrigation) have raised the issue of how these inputs can be used most effectively. Subsistence agricultural systems that evolved in low-fossil-fuel-energy environments might contain features that optimize the use of resources and/or reduce the risk of crop failure. One such feature is the high diversity of crops frequently planted side-by-side in traditional tropical agricultural systems.

The term intercropping has been widely used to designate simultaneous planting of more than one species in the same field at the same time, while "multiple cropping" is a more general term that includes relay and series planting of the same or different species (Dalrymple 1971, Beets 1975, Norman 1979). Kass (1978) used "polyculture" in reference to any situation in which two or more crops are simultaneously grown together; "multiple cropping," to any situation in which more than one crop is grown on a given area in one year; and "intercropping," to simultaneous alternate-row plantings. The planting patterns used in this study sometimes mixed species within rows, and therefore do not conform to Kass's use of the term intercrop, but they do fit the generally accepted use of the word by other researchers.

Intercropping, and other forms of multiple cropping, have been credited with increased productivity, reduced risk of crop failure, and reduced incidence of pests and diseases (Janzen 1973, Dasman et al. 1974, Trenbath 1975a, Gibson and Jones 1976, Papendick et al. 1976,

Pimentel 1976, Sanchez 1976). These systems are looked to with great hope as potentially stable, productive, low-energy-input cropping systems for the developing tropics.

Productivity in Crop Mixtures

The experimental evidence to back up claims of increased productivity in crop mixtures is abundant, but the results are seriously confused by the varying methods used to determine intercrop planting densities and compare productivities. Kass (1978) gave an excellent review of the massive literature on this topic. Regarding yield and resource use, he concluded that by many measures polycultures are clearly superior to monocultures in terms of yield. Trenbath (1974) reviewed 344 data papers in which 60 percent of the two-crop mixtures studied yielded more than the mean yield of corresponding monocultures. Significantly more of the 572 mixtures reviewed by van den Bergh (1968) yielded more than monocultures as measured by the Land Equivalent Ratio (see below) than yielded less than monocultures.

Trenbath (1977) reviewed possible mechanisms responsible for productivity increases in mixtures. Competition for light, water, and nutrients may be reduced through temporal partitioning of growth and resource demand, spatial partitioning of root and leaf systems, differences in limiting factor response curves (different resource "requirements"), shading and leaf angle effects on light utilization, and shading effects on water use. These mechanisms typically result in higher-than-monoculture yields of one species (the "aggressor"), the lower-than-monoculture yields of the second species (the "subordinate"), and increased productivity of the system as a whole.

Increased productivity in mixtures may also be due to allelopathic or allelophilic interactions, changes in the rhizosphere flora, mechanical factors (e.g., wind protection and support for understory crops), and reduced pest and disease impact as a result of reduced resource concentration and microclimate effects (Trenbath 1974). Mixtures also have the capacity for compensatory growth, or the exploitation by one species of resources liberated through the demise of an unlike neighbor.

Resource Partitioning and Competition Reduction

The most convincing body of evidence of resource partitioning in crop mixtures regards spatial partitioning of rooting zones (Kurtz et al. 1952, Litav and Harper 1967, O'Brien et al. 1967, Whittington and O'Brian 1968, Ellern et al. 1970, Raper and Barber 1970, Baldwin and Tinker 1972, Kauraw and Minko 1972, Portas 1973, Nelliat et al. 1974, Allmaras et al. 1975a, 1975b, Trenbath 1975b, Nair 1979). Other aspects of competition reduction have been less well studied. Complementarity of nutritional and water demands was suggested by Glover (1948, 1959), Kolb (1962), and Davies and Snaydon (1973). Reduced competition for nitrogen may be especially important in mixtures containing legumes (de Wit et al. 1966). Light distribution in canopies, reduced leaf angles in the lower canopy, and displacement of shade-adapted species with large leaves and lower optimum leaf temperatures lower in the canopy can all contribute to improved light use efficiency in mixed crop systems (Monteith 1965, Parkhurst and Loucks 1972, Trenbath 1974, Terjung and Louie 1973). Temporal partitioning of leaf and root development and grain-filling was thought to be responsible for high intercropping yields in two studies (van den Bergh and de Wit 1960, Kassam and Stockinger

1973). Labor inputs have been quantified in a number of studies (reviewed by Kass 1978), but the results are not clear, and there is no obvious reason to expect labor inputs to be reduced in intercropping systems. In the studies reviewed by Kass, labor use was usually higher in intercrops than monocultures, but the reverse was sometimes also found to be true. The reasons for differences in labor use have not been investigated.

A number of researchers have proposed models and/or field measures of competition among crops in mixtures. Vandermeer (1982) obtained whole-system yield graphs (at all density combinations) from intercrop competition equations based on the Lotka-Volterra equations. He also showed (1981) that the same nonlinearity of yield-density functions that allows species coexistence in nature (Lotka-Volterra equations) also occurs in intercrops that yield more than corresponding monocultures (Land Equivalent Ratio > 1). That the mathematical expression for nonlinearity is of the same form in both cases should perhaps not, however, be taken as proof that the competitive function and Land Equivalent Ratio are "mathematically identical" criteria, as Vandermeer states.

Other models of competition are not derived from the Lotka-Volterra equations, and seem to lack a theoretical common ground; the relations between de Wit's (1960) crowding coefficient, McGilchrist's (1965) measure of aggressivity in mixtures, Donald's (1963) competitive index, and Willey and Rao's (1980) competitive ratio are not clear. Part of the confusion stems from the varying use of per-plant and per-area measures, and the lack of differentiation between competition within a species and competition among species, which creates difficulties in situations where overall planting density is not held constant. The

de Wit and Lotka-Volterra equations contain competition coefficients that vary under different growing conditions and overall planting densities; the other three measures do not contain such coefficients, and are much more readily applied to field observations. Only the de Wit and Lotka-Volterra equations can be easily expanded to include more than two species, however.

As our awareness of the complexity of biological interactions in intercrops increases, the use of simplified models and indices of competition to explain yield differences become less and less tenable on theoretical grounds. It is nevertheless desirable that researchers agree on a few measures of species and system performance that are robust under varying planting densities, crop composition, and number of crops interplanted.

Pests and Diseases

Insect ecology has contributed much to our understanding of mechanisms operating to determine pest levels and stabilities in agricultural systems (see the numerous reviews listed above). Due to the many complex interactions involved, differences in pest mobilities, plot size effects, and many other factors, generalizations cannot be made regarding the effects of intercropping on pests and diseases. The field data available support this conclusion: Kass (1978) and Trenbath (1976) gave numerous examples of both increased and decreased pests and diseases in intercrop systems. Pest stability is much less well researched; virtually no data are available on that topic, and both stabilizing and destabilizing mechanisms may operate in intercrop systems.

Stability and Risk

Risk reduction is an especially critical issue in the developing tropics, where obtaining at least a minimum harvest each year may be more important than obtaining maximum average yield over a period of several years. The term risk is not synonymous with ecological (in)stability, however. Risk contains both a productivity and a stability component, since a system having generally high productivity is less likely to fall below a given disaster level than a less-productive system. Productivity rather than stability may be the most important factor determining degree of risk (Rao and Willey 1980). Stability rather than risk was the parameter evaluated in the present study, but inferences regarding risk reduction are drawn in the discussion.

Stability in intercrop systems is much less well-researched than productivity, resource partitioning, and pest and disease levels. Two mechanisms underlying the hypothetically greater stability of intercrops are compensatory growth and greater stability of pest populations. Donald (1963) found that in 51 of 70 mixtures examined, per-plant yield of one component increased and the other decreased (compared to monocultures), but it was not possible to distinguish between uneven resource partitioning and compensatory growth as possible causes of the imbalance. Few clear examples exist in the literature, but increased growth of understory plants in response to natural and artificial damage to the overstory was reported by Fisher (1977) and Liboon et al. (1976).

Trenbath (1974) reviewed several data papers in which seed yield stability of a mixture of two genotypes was greater than that of the

more stable component. This situation is the exception rather than the rule; he stated that the stability of mixtures usually lies between that of the component species or genotypes. Kass (1978) cited several studies in which year-to-year variability was less in mixtures than in monocultures. The usual measure of yield variability in such studies has been the coefficient of variation (C.V.) over time or space.

Rao and Willey (1980) found that stability of a sorghum-pigeonpea intercrop in 51 experiments over a period of six years was higher than either monoculture (C.V.=39 perent in intercrop, 49 and 44 percent in monocultures), and very slightly higher than that of a weighted mean of the monocultures (C.V.=39 vs. 42 percent). These differences are not striking, however, and are confounded by the fact that the intercrop consisted of full stands of both component crops. Rao and Willey also determined degree of regression of intercrop and monoculture yields with a site favorability index, and found that the intercrop system response was intermediate between that of the less responsive sorghum and the more responsive pigeonpea. Risk of crop failure was much lower in intercrop than monoculture, due primarily to differences in productivity.

Methodological Problems

The major difficulty with interpretation of the wealth of experimental intercropping data concerns uncontrolled planting densities. Overall level of biological activity in intercrops may be higher due to planting more seed of species that grow into larger plants for seeds of small plants. This increased "functional density" (density

of biological function) may bias yield results in favor of the intercrop. Fisher (1977) found, for example, no yield advantage in maize-bean mixtures beyond that due to increased planting densities. Increased functional density of plants also leads to early cessation of growth and altered microclimate (Pimentel et al. 1962), reduced root/shoot ratios (Milthorpe and Moorby 1975) and increased risk of moisture stress (Dowker 1963, Milthorpe and Moorby 1975). The question arises as to how effects of inter- and intraspecific competition can be compared without altering overall planting density. The problem becomes critical for species of very different plant size, and is a serious factor that confounds the results of most intercropping experiments.

One of three methods is normally used to determine densities of the two interplanted species (Haizel 1974). In the additive method, normal full stands of two crops are superimposed to give a double stand. In the substitutive method, a given number of individuals of species A are replaced by the same number of individuals of species B, giving either a less or more full stand than normal, depending on which species uses more resources per plant. In the replacement series method (Osiru and Willey 1972, Willey and Osiru 1972), a given fraction of the optimum stand of species A is replaced by the same fraction of the optimum stand of species B. In addition to the above three methods, in many intercropping studies the component species are planted in unusual combinations of densities. Any of these experimental designs might be suitable if one's goal is to find the crop or crop combination having maximum yield. Only the "replacement series" method controls for overall functional density of plants, however, and can show the effects of spatial diversity (not density) on system structure and function.

A second problem with the literature on intercropping concerns methods used to compare intercrop and monoculture yields. The simplest method is to compare the total yield from an intercrop with that from monocultures of the component crops. Trenbath (1974), in a review of over 300 studies, found that situations in which the intercrop yielded either more or less than both components ("transgressive yielding") were relatively rare. When two crops have been planted in equal proportions in the mixture (by either the substitutive or replacement method), the intercrop yield is most often compared with the mean yield of the two monocultures (also known as the mid-monoculture yield or the sum of the half-hectare yields). When used with the substitutive design, the meaning of this comparison is not clear, since the density of the species that was "substituted in" is usually not equal to half its density in monoculture.

The most common method for comparing intercrop and monoculture yields is the Land Equivalent Ratio (LER), also called the Relative Yield Total (RYT) and defined as the sum of the component species' per-hectare yield in intercrop, divided by per-hectare yield in optimum-density monoculture. Each species' ratio represents the area of monoculture required to give the same yield as one hectare of intercrop; the sum of the ratios represents the area required to equal the yield of all crops from one hectare of intercrop. Land Equivalent Ratio has the advantage that it is easy to conceptualize and calculate. One disadvantage is that it may have little meaning when applied to systems having different planting densities, especially if the monocultures are more sparsely planted than the intercrops, as is very often the case, giving a falsely high LER. Land Equivalent Ratio also should

not be used when intercrop/monoculture yield differences are large, because yield increases in the intercrop are given greater weight than decreases (an artifact of the ratio calculations). For example, if species A yields twice as much in intercrop as in monoculture ($LER_A = 2$) but species B yields four times as much in monoculture as in intercrop ($LER_B = .25$), the overall performance of the intercrop is judged highly favorable (LER = 2.25). Perhaps the most serious criticism of LER is that it gives equal weight to both high- and low-yielding components of an intercrop. This weighting has been justified by the argument that both crops may be necessary to the farmer, but can result in high LER's in situations where a minor crop failed in the monoculture. Table 1 gives a hypothetical example of this situation, where LER = 2.3 even though the mid-monoculture yield was greater than that of the intercrop! This distortion occurs because the species' performances are not weighted by yield.

A New Index

A more meaningful index of intercrop performance than the area of land required to produce the exact same yield of all crops as the intercrop would be the yield difference of intercrops and monocultures grown on the same land area. Yield could be expressed in terms of any parameter of interest (biomass, kcals, protein, money, etc.). I propose to call this new index the Yield Equivalent Ratio (YER) because it is the ratio of yields from equivalent land areas, in contrast to the Land Equivalent Ratio, which is the ratio of land areas for equivalent yields. YER is defined as the ratio of intercrop yield on an area to yield of

Table 1. Distortion of Land Equivalent Ratio (LER) by failure of a minor crop in monoculture. This hypothetical example assumes equal planting densities (by the substitute or replacement methods) in the intercrop.

	SPECIES 1	SPECIES 2	TOTAL YIELD
A. INTERCROP YIELD	300	200	500
B. MONOCULTURE YIELD	1000	100	550
A/B	.3	2	

LER = .3 + 2 = 2.3

monocultures of the component crops grown on the same area, divided among the monocultures in the same proportion as their intercrop planting proportions. Planting proportions are expressed as percent of optimum monoculture stands, and should add to one. With modifications the ratio could also be applied where planting proportions added to more than one (overpacked intercrops); the resulting ratio would then reflect packing effects as well as diversity effects.

In mathematical form,

$$YER = \frac{Y_{1,I} + Y_{2,I} + Y_{3,I} + \ldots Y_{i,I}}{(Y_{1,M} \cdot p_1) + (Y_{2,M} \cdot p_2) + (Y_{3,M} \cdot p_3) + \ldots (Y_{i,M} \cdot p_i)}$$

where $Y_{i,I}$ = per-area yield of species i in intercrop

$Y_{i,M}$ = per-area yield of species i in optimum-density monoculture

p_i = proportion of optimum density monoculture planted of species i planted in the intercrop

Yield Equivalent Ratios greater than one indicate that greater yield per area is obtained from intercropping than from the same area divided among monocultures of the same functional density, and reflect reduced competition or other effects associated with increased spatial diversity. When applied to a half-full-stand + half-full-stand mixture of two crops, YER reduces to the ratio of intercrop yield to the mid-monoculture yield, a comparison that has been widely used to evaluate the performance of two-crop intercrops (Trenbath 1974). Unlike LER, YER can be evaluated statistically through comparisons of the numerator and denominator.

Performance of each species in intercrop and monoculture can also be compared with YERs calculated on the basis of intercrop and monoculture yields of that species only:

$$YER_{species\ 1} = \frac{Y_{1,I}}{Y_{1M} \cdot P_1}$$

Hypotheses

The goal of this study was to compare the productivity and stability of diverse and simple systems of equivalent density, and to elucidate some of the mechanisms responsible for differences found. The following hypotheses and corollaries formed a framework for the study.

Hypothesis 1. Productivity of diverse cropping systems is greater than a weighted mean of monocultures of their component crops.

Corollary A. Intercrop productivity is intermediate between that of the most productive and least productive components.

Corollary B. The greater the intensity of stress (the less productive the growing conditions), the greater the productivity advantage of intercrops compared with a weighted mean of corresponding monocultures.

Hypothesis 2. Yield stability (constancy) of diverse systems is greater than the stability of a weighted mean of the yields of corresponding monocultures.

Corollary A. Intercrop stability is intermediate between that of its most stable and least stable components.

Corollary B. Stability of all systems is greatest under the most productive conditions (lowest intensity of stress).

Hypothesis 3. Some species are more productive in diverse systems than in monoculture; others are more productive in monoculture.

Hypothesis 4. Some species are more stable in diverse systems than in monoculture; others are more stable in monoculture.

Hypothesis 5. Pest and disease levels are lower and pest stability higher in diverse systems than in monoculture.

Hypothesis 6. Efficiency of resource use (light, water, nutrients, human labor) is greater in diverse systems than in monocultures.

Corollary A. Root and leaf systems of different species occupy different vertical zones, and vertical profiles of leaves and roots are more evenly filled in diverse systems than in monocultures.

Corollary B. Compensation occurs among components of diverse systems; low productivity of one species causes increased productivity of others.

Corollary C. Intercrop systems composed of species with unlike resource-response curves and temporal growth patterns have the greatest productivity advantage compared with corresponding monocultures.

Hypothesis 7. Natural successional vegetation of the same age as the crop systems is the most stable and productive of all systems and has the most evenly-filled root and leaf profiles.

Experimental Approach to the Hypotheses

Intercrop systems selected for study were based on those commonly used in the area. A four-crop system was included as a more diverse system than the usual two-crop intercrop systems. Planting densities were determined by the replacement method in order to maintain equal functional densities. Monocultures of each crop were grown, and successional vegetation and bare ground plots were included as controls. Four "stress treatments" were applied: fertilization, pesticide spraying, defoliation, and watering. Effects of these four types of stressors were compared with a control treatment that was an imitation of local, low-energy-input farming practices.

Response parameters included measures of biomass accretion and distribution, pest and disease incidence, and resource use. Hypotheses were tested concerning system performance, species performance in various systems, and comparisons of intercrop performance with that of corresponding monocultures.

The Tanzanian Agricultural Setting

Overview

The economy of Tanzania is largely dependent upon the productivity of its small-scale farmers, who comprise an estimated 90 percent of the population. Agriculture produces 40 percent of the country's GNP and 80 percent of its import earnings (Witucki 1978). Fifty percent of food production is consumed on-farm. Tanzania is a net importer of food, and a pattern of frequent food shortages has been documented from 1850 to recent years (Brooke 1967a, 1967b). The most frequent cause of

crop failure over this period was drought, but other causes included excessive rainfall, locusts, birds, and armyworms. The level and stability of agricultural production on small farms are therefore questions of prime importance both to the national economy and the welfare of the Tanzanian people.

Agricultural change has been rapid in Tanzania in the 21 years since independence. In 1967 President Nyerere introduced a socialist development policy called ujamaa. Development efforts were concentrated in newly formed ujamaa villages, consolidated from previously scattered settlements to facilitate introduction of improved social services and agricultural technology (McKay 1968). This unusual development approach and the philosophy of self-reliance are most eloquently expressed in Nyerere's own writings (1973, 1974).

Under the new development approach, agricultural productivity rose at a rate exceeding the population growth rate from 1965 to 1975 (Ruthenberg 1973, Witucki 1978). A campaign to increase farmer's agricultural efforts on both private and communal fields stimulated small farmer activity. International aid projects provided assistance for improved seed, crop agronomy, and appropriate agricultural technology. The most notable project was the National Maize Project, begun in 1975. Its goal was to increase maize production in favorable areas through improved seed and fertilizer inputs and improved crop management (Fortmann 1976). Villages and individuals were particularly encouraged to increase the area of maize and cotton planted and to plant maize at higher densities. In many cases partially subsidized inputs including improved seeds, fertilizer, pesticide, and tractors were supplied.

Several years of bad weather in the mid-1970's, involvement in the Uganda war in 1978-1979, increasing oil prices, and internal management problems all contributed to a reversal of the progress made from 1965 to 1975. Tanzania's foreign exchange situation is now extremely serious, and the country is highly dependent on foreign grants and loans to finance the present five-year development plan (Witucki 1978).

In the present energy and economic environment, the best strategy for agricultural development may be a two-pronged one. Higher productivity through use of fossil-fuel inputs is desirable where economically feasible; other, low-risk systems that make the most efficient use of available resources are also desirable to minimize small farmer dependence on unpredictable fossil-fuel-based resources. Development of traditional, diverse cropping systems for increased productivity may be one way to achieve this second goal. Identification of specific mechanisms that may operate in those systems to reduce labor demand, reduce risk of pest and disease attack, increase efficiency of water, light, and nutrient use, and reduce the risk of crop failure is the first step in the process of adapting traditional systems for increased productivity without increasing risks for small farmers.

Traditional agricultural systems in Tanzania are extremely diverse and highly adapted to the local climate and soils (Ruthenberg 1964, 1968). Fortmann (1976) surveyed 96 farmers in Morogoro District (the district where this study was conducted) and found that 64 percent of the area planted to maize was intercropped with one or more other crops. Seventy percent of total maize area planted had no improved inputs; another

22 percent received only improved seed input, and a very low percent was fertilized. The villages she surveyed were generally located on favorable mountain slopes and river floodplains. The most common species intercropped with maize in those areas were beans, rice, sunflower, and bananas.

Survey of Local Crop Systems

Local farmers' crop systems and cultural practices were used to the greatest extent possible in this study, for three reasons. First, results of this study will be of more practical value in suggesting possible changes and improvements in cropping systems if they are taken from authentic systems widely used by farmers. Second, little experimental ecological research has been done with indigenous systems (and cultural practices), especially intercropping system composed of three or more species. Third, if intercropping is advantageous in terms of stability and yield, one might hypothesize that it is most advantageous for the unpredictable and low-resource environments in which small-scale farmers operate, and for cropping systems that have persisted over time, presumably because farmers found them to be successful.

Methods

To determine the most common cropping systems in the study area, I conducted 30 interviews with farmers in 15 villages in the Kilosa district of Morogoro Region in October and November, 1978. The District Agricultural Development Officer of Kilosa District kindly accompanied me, provided transportation, and introduced me to village leaders.

Selection of farmers was not random, but rather an attempt was made to select experienced, longtime residents who were willing and able to provide detailed descriptions of their farming practices. Interviewees were actually selected by the Village Chairman (or his representative) or the village agricultural officer, and so may represent the modernized sector of the farming population. The sample was approximately 30 percent female and 70 percent male.

Interviewees were asked to describe qualitatively each of the fields they had cultivated the previous year, including species composition, plant arrangement, cultivation practices, and use of high-energy inputs (seeds, tractors, fertilizer, pesticide). They were also asked how long they had used each system and what they felt its advantages and disadvantages were, particularly with regard to mixing species in the same field. Finally, they were asked to describe systems they had used in the past, and to tell what they felt their main agricultural problems were. Survey results pertaining to crop combinations used and farmers' perceptions of their advantages and disadvantages are reported here.

Results

The survey revealed that an agricultural transition of surprising depth and breadth is taking place in the surveyed villages, that is probably typical of the situation in villages throughout Tanzania. Farmers' ideas about their traditional cropping systems are changing under the influence of agricultural officers and programs aimed at introducing Green Revolution technology and increasing the area of

maize and cotton planted. Farmers are experimenting with the new systems, but almost always keep some fields planted in traditional patterns.

Great diversity of cropping systems was present, both among each farmer's fields and among different farmers' fields. All 30 farmers used more than one cropping system; a maximum of 9 and mean of 3.9 systems per farmer were reported. Almost all farmers (28 out of 30) planted at least one kind of monoculture, of which maize was the most common (22 farmers out of 28). More farmers used monocots as monocultures than used dicots as monocultures (26 and 18, respectively. In addition to the major-season monoculture field crops, many farmers (10) relay-planted bean monocultures after monocultures of Gramineae, and many (9 of 20 queried) planted a mixed vegetable garden, invariably composed of several species planted in separate rows, or more commonly separate sections, of the garden. Most farmers interviewed (19 of 30) cultivated some fields as monocultures and some as intercrop systems. Of the remaining 11 farmers, 9 planted exclusively monocultures and two planted exclusively intercrops.

Most farmers reported that the monoculture systems were relatively new in the last 2-20 years, although sorghum, cassava, greengram, and sparsely spaced maize were mentioned as monoculture systems used in the past that are less widespread now. Many farmers (11 of 30) also described intercrop combinations they had planted previously but no longer used at the time of the interview. Two farmers mentioned that they had changed from scattered to row planting, and two more noted that they used to plant two or more species in the same hole but now planted them in separate holes in the same field.

A total of 33 intercrop species combinations were given by the interviewed farmers; these are broadly categorized and listed in Table 2. The great majority of the systems were combinations of monocots and dicots; only six of the 33 intercrop systems were all-monocot or all-dicot. Three all-grass systems were mentioned, one being in quite widespread use (maize-sorghum, 8 of 33 farmers). Three systems containing no monocots were used, all of them composed of one legume and one "other dicot" (= not Leguminosae or Cucurbitaceae). Interestingly, two of the "other dicots" were tall species (sunflower and cassava) which may function much like graminaceous species in these all-dicot intercrop systems.

Grass-legume systems accounted for 13 and grass-legume-cucurbit systems for 8 more, of the 33 intercrop combinations. Many of these contained more than one grass and/or legume. In addition to the grass-legume and grass-legume-cucurbit systems, six other monocot-dicot systems were given: two grass-cucurbit, two grass-other dicot, and two grass-legume-other dicot. The most common spatial arrangement for monocot-dicot systems was relatively widely spaced rows of grass species (in alternate rows if more than one grass species was present) with legumes or other dicots scattered, or in rows, between the rows of graminaceous species. Cucurbits were described as being planted "here and there" or at several-meter intervals between the rows of monocot species.

Interviewees' responses were mixed regarding the advantages and disadvantages of intercropping; 24 of the 30 farmers interviewed did, however, have one or more comments to make on the subject. The responses

Table 2. Intercropping systems used by 30 Morogoro Region farmers. Crop combinations that farmers said they used in the past are included.

NUMBER OF RESPONDENTS	MAIZE (*Zea mays*)	SORGHUM (*Sorghum bicolor*)	BULRUSH MILLET (*Pennisetum typhoides*)	RICE (*Oryza sativa*)	COWPEA (*Vigna unguiculata*)	FIWI (*Lablab niger*)	BEANS (*Phaseolus vulgaris*)	GREENGRAM (*Phaseolus aureus*)	PIGEONPEA (*Cajanus cajun*)	PEANUTS (*Arachis hypogaea*)	SOYBEANS (*Glycine max*)	PUMPKIN (*Cucurbita* spp.)	GOURD (*Lagenaria siceraria*)	CASTOR (*Ricinus communis*)	SUNFLOWER (*Helianthus anuus*)	CASSAVA (*Manihot esculenta*)	SESAME (*Sesamum indicum*)	COTTON (*Gossypium* spp.)
ALL GRAMINEAE																		
8	X	X																
1	X		X															
1	X			X														
NO GRAMINEAE																		
1					X													X
1					X											X		
1							X								X			
GRAMINEAE + LEGUMINOSAE																		
8	X				X													
4	X					X												
4		X				X												
3		X			X													
2	X						X											

Table 2--extended.

1	X						X								
1	X							X							
1	X								X						
1	X									X					
1	X	X		X											
2	X	X			X										
1	X	X	X	X											
1	X	X	X	X			X								
GRAMINEAE + CUCURBITACEAE															
9	X										X				
2	X											X			
GRAMINEAE + OTHER DICOT															
2	X												X		
1	X														X
GRAMINEAE + LEGUMINOSAE + CUCURBITACEAE															
3	X			X							X				
2	X				X						X				
1	X			X	X						X				
1	X	X		X		X					X				
1		X		X			X				X				
2	X	X		X	X						X				
1	X	X		X	X		X				X				
1	X			X	X						X		X		
GRAMINEAE + LEGUMINOSAE + OTHER DICOT															
1	X				X								X		
1	X					X								X	

were categorized, and for the sake of simplicity the specific intercrop systems involved were ignored. In almost all cases the farmer was comparing maize-legume or maize-legume-cucurbit systems with maize monoculture or monocultures of the species comprising the intercrop system.

Of nine farmers who mentioned intercrop/monoculture yield differences, seven said intercrops had higher yield than monocultures and two said monocultures yield more. Two farmers preferred intercrops because of the diversity of crops one harvests and the early harvest of legumes from intercrop systems. Two interviewees said that the chance of total crop failure was reduced in intercrops, but ten noted that at least one crop is likely to fail in an intercrop. Of those ten, six were referring to the high risk of maize failure in two-grass systems, and one gave shading as the reason. One farmer felt that maize is stronger in intercrops in general. These comments are not necessarily incompatible: risk of losing one crop and risk of losing all crops are not the same thing, and it is quite possible that maize is at high risk in all-monocot systems but not in other intercrop combinations.

One farmer said intercrop was better than monoculture during drought, and one noticed reduced erosion on intercropped fields. One stated that intercrops had more pests than monocultures; two said there was no difference. Two said monocultures had more weeds than (maize-pumpkin) intercrops; five said there was no difference.

The numbers of farmers who noted higher or lower labor requirements for various tasks in intercrops compared to monocultures were as follows: planting--three (intercrop more), five (less), one (no difference); weeding--six (intercrop more), three (less), one (no difference);

harvest--one (intercrop more), one (less); total labor--two (intercrop more), one (less). These results suggest that intercrops may be easier to plant but harder to weed than monocultures. One interviewee felt that monocultures are preferable for village communal fields (ujamaa fields) because they are easier to manage when many people are involved. Finally, three farmers mentioned crop mixtures that do not work well: maize-fiwi bean, maize-rice, and any intercrop with cassava. Two more admonished against planting two species in the same hole; one of these specified that two grasses or two legumes should not share the same hole.

Planting density is an issue of some interest in Tanzania because farmers are being encouraged to plant at higher densities than they traditionally have. Of six farmers who mentioned planting density, five preferred sparse to dense plantings for the following reasons: survives better in drought (four respondents); wilts less (one); lodges less in drought (one); stronger roots (one); easier to plant (1). One farmer commented that sparse plantings yield the same as dense; one that insect levels are the same in both; and one that weed growth is the same in both. One farmer preferred dense plantings because of higher yields in wet years.

CHAPTER TWO
METHODS

The Study Site

Location and History

The study was conducted during the 1978 and 1979 growing seasons (called Year 1 and Year 2) near the town of Morogoro, Tanzania. At 38°E and 7°S, Morogoro lies approximately 200 km west of Dar es Salaam and the Indian Ocean, and sits at the base of the Uluguru mountain range.

Field plots occupied 2 ha on the campus of the Faculty of Agriculture, Forestry, and Veterinary Science, a branch of the University of Dar es Salaam situated a few kilometers from Morogoro town. The plots were located approximately 1 km north of the main campus buildings, occupying nearly flat land 550 m in elevation, 60 m above the present level of the Ngerengere River to the west, and between small streams flowing from the mountains toward the river. The plots were bordered on three sides by a strip of young successional vegetation and by a dirt road on the fourth. Beyond the successional strip was a variety of field crop and pasture experiments.

The land on which the study site was located was part of the Tanke Sisal Estate until the founding of the Faculty of Agriculture in 1970, after which it was used for agricultural experiments. Small patches of *Brachystegia*- and *Combretum*-dominant miombo woodland occur

locally at uncultivated sites and suggest that this fire-adapted vegetation once covered the area. The study site was in fallow for two years preceding this study and was covered with a dense 2-3 m tall brush dominated by a diverse mixture of grasses, including _Chloris gayana_, _Panicum maximum_, _Digitaria scalarum_, _Rottboellia exaltata_, and _Cynodon dactylon_. The successional regrowth also contained occasional sedges (_Cyperus rotunda_ and _C. tuberosus_), and an understory of herbaceous and occasionally woody dicots including _Celosia trigyna_ and _C. laxa_, _Bidens pilosa_, _Sonchus examiculatus_, _Crotelaria_ spp., _Ipomoea mombasana_ and _I. tenurostris_, _Galinosoga parviflora_, _Tridax procumbens_, _Amaranthus_ spp., and many others. Several small vines were present, but they did not dominate the grassy overstory.

Climate

Amount and distribution of rainfall are the most critical climatic factors affecting crop production in the Morogoro area. As would be expected for a site of low latitude and moderate elevation, temperature and solar radiation do not limit the production of the major food crops. Slightly lower temperatures occur in June and July (mean 21-22°C) than during the rest of the year (mean 23-26°C). Lowest insolation is during the high-cloud-cover rainy period from March through May (Jackson 1975b).

Rainfall patterns in Tanzania result from the interaction of two seasonal monsoons that dictate the movement of the intertropical convergence zone, and complex local convergence patterns (Jackson 1975a). Most of the midelevation Central Plateau of Tanzania is in the Tropical

Very Dry Forest life zone of Holdrige (1967), receiving 400-900 mm annual rainfall in a single season from approximately November to May. Morogoro, because of its proximity to the Uluguru Mountains, receives about 1000 mm annually, distributed rather unpredictably from November to May, and is therefore at the edge of the Tropical Dry Forest life zone. In most years a one- to three-week dry period sufficient to kill young crops occurs in January or February. This short drought divides the season into the "short rains" (November to January), generally considered too unpredictable to be relied upon for the main crop, and the "long rains," beginning in late February or March, during which most agricultural activity takes place. The unpredictability of both amount and distribution of rainfall makes annual cropping a risky occupation on the Central Plateau, although less so in Morogoro due to the local higher total precipitation.

The rains were considered by local people to be slightly heavier than average in both study years. Tanzania Meteorological Station No. 96-3776 (less than 1 km from the study site) recorded 1117 mm for 1978 and 735/882 mm for the main growing season from January through July in 1978 and 1979, respectively. Measures of precipitation taken daily on the site between March 27 and July 28, 1978,were only 3 percent higher than those from the meteorological station.

Soils

Soils on the study site are thought to be the product of uplift, colluvial and alluvial deposition, and erosion by water. The Morogoro area is geologically young compared with the sountern part of Tanzania

(Temple 1975, Pratt and Gwynne 1978). The yellow-red soil (color 7.5YR 4/6) was tentatively identified as an alfisol. Alfisols and oxisols are both present in the Morogoro area (National Academy of Science 1972, Dregne 1976) but subsurface clay accumulation (see below), predominance of kaolinite clays, and moderate levels of weatherable minerals at the site (Nicholaides and King 1980) suggest that the soil is an alfisol.

To determine the overall nutrient status of the soil, 33 composite samples of surface soil (10, 0-15 cm deep cores from each of 33, 15 x 21 m experimental plots) were collected. They were analyzed by the Department of Soil Science in Morogoro for pH (1:1 in water), total nitrogen (micro-Kjeldahl, Black 1965), available phosphorus (Bray and Kurtz 1945, method no. 1), exchangeable bases, and organic carbon. While the soils are not excessively acidic, they are low in total nitrogen, available phosphorus, and organic carbon, and have low cation exchange capacity and high carbon/nitrogen ratio. Ranges and means are given in Table 3. The broad ranges of element concentrations and pH indicate high spatial heterogeneity, but no clear spatial trends across the study site were evident for any of the parameters.

In addition, the distinguishable soil horizons were sampled to a depth of 100-130 cm in five soil pits located throughout the study site (Figure 1). Determinations of pH, organic carbon, total nitrogen, and particle size distribution were made by the Department of Soil Science in Morogoro. Particle size distribution was by the Bouyoucous hydrometer method; other methods were as above. Values of pH, organic carbon, and total nitrogen in the top 20 cm agreed with those from the

Table 3. Surface soil pH, total N, available P, organic C, and base concentrations. Range and mean are given for 33 composite samples of 10 0-15 cm deep cores each, except for total N, where three anomalously low readings were discarded.

SOIL PARAMETER	RANGE	MEAN
pH	4.8 - 6.0	
TOTAL N (percent)	.05 - .10	.08
AVAILABLE P (PPM)	.2 - 2.0	1.14
ORGANIC C (percent)	.8 - 1.2	1.0
Na (me/100 g soil)	.09 - .27	.13
K (me/100 g soil)	.90 - 2.79	1.76
Ca (me/100 g soil)	9.08 - 29.33	17.45
Mg (me/100 g soil)	.47 - 12.25	4.95

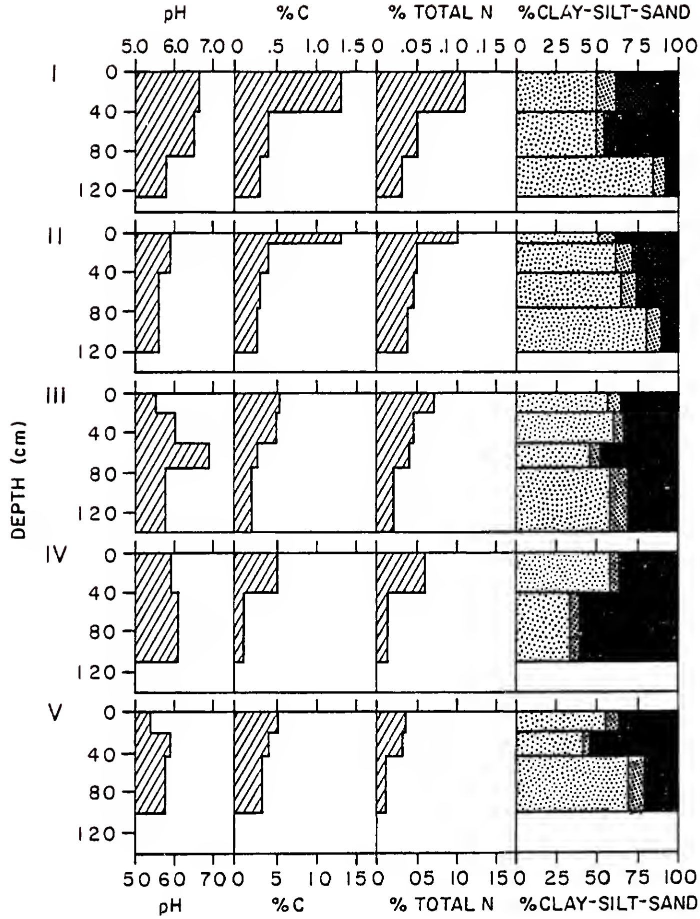

Figure 1. pH, percent C, percent total N, and particle size distribution in five soil profiles (I-V) taken at the study site.

composite samples. Organic carbon and total nitrogen were very low below 20-40 cm in all profiles: less than 0.5 percent organic carbon (minimum 0.1 percent) and less than 0.05 percent total nitrogen (minimum 0.01 percent). Profiles I and II, located in the slightly elevated southeast corner of the site, had increasing clay particles and decreasing pH below 80 cm, suggesting an argyllic horizon, but profiles III, IV and V did not show consistent trends in pH and particle size distribution with depth. The silt fraction was consistently low (less than 12 percent), and in all profiles the higher pH values were associated with a greater sand fraction. Soil texture was categorized as clay to sandy clay.

Some parts of the site had a tendency to waterlog, but most of the site experienced only temporary standing water after long and/or hard rainy periods.

Experimental Design

Crop System, Stress Treatments, and Planting Density

Based on the farmer survey, four intercrop combinations were chosen for study: maize-sorghum, maize-cowpea, maize-pumpkin, and a four-crop system, maize-sorghum-cowpea-pumpkin. These four represent a range of types of crop combinations (grass-grass, grass-legume, grass-cucurbit, and diverse grass-legume-cucurbit). For comparison, each crop was also grown as a monoculture. Sorghum, cowpea, and pumpkin densities were those recommended by the Ministry of Agriculture for local conditions, while maize monoculture was grown both at the

recommended density and half the recommended density (hereon called "sparse maize"). Two more systems were included as controls for measurements of yield, Leaf Area Index (LAI), weed growth, soil moisture, and recovery after defoliation: natural succession (on ground prepared the same as the rest), and a vegetation-free or "bare ground" system. In the second year of the study the maize-sorghum, maize-cowpea, maize-pumpkin, sparse maize, and bare ground systems were omitted to allow greater replication and inclusion of more "stress treatments."

The planting density of each crop in the intercrop system was adjusted so that all crop systems except sparse maize had the same functional density of plants; that is, differences in system structure and function were due solely to differences in diverstiy and not to differences in crowding or plant density. Equal functional density was achieved by planting the species in a mixture in proportions adding to one, for example one-half maize and one-half sorghum. The proportion allocated to each species, multiplied by its monoculture or full-stand density, gives that crop's planting density in the intercrop. In the example given, a hectare of maize-sorghum intercrop would contain the same number of maize plants as one-half hectare of maize monoculture (being planted at half the monoculture density), and the same number of sorghum plants as one-half hectare of sorghum monoculture. This method of determining planting density so that all systems have the same functional density is based on the "replacement series" methods of Willey and Osiru (1972). To compare performance of either species or whole systems, yields (or other measures) are weighted according to planting density.

The proportions for mixtures used in this study were based on the farmer interviews, and were as follows: maize-sorghum (1/2 + 1/2), maize-cowpea (1/2 + 1/2), maize-pumpkin (2/3 + 1/3), four-crop (1/4 + 1/4 + 1/4 + 1/4). The actual planting densities these proportions represent, and the full-stand densities on which they are based, are given in Table 4. Since individuals of different species do not replace each other one-to-one in this method, total plant densities of the systems differ.

Plant arrangements in the intercrop systems are shown in Figure 2, and the spacing for each species in both intercrop and monoculture systems is given in Table 4. Intercrop arrangements were patterned after those described by local farmers, with the exception of maize-sorghum, which consisted of two rows of sorghum 40 cm apart alternating with one row of maize. This arrangement prevented crowding of sorghum within rows and gave a more even spatial distribution than would alternating single rows. Local farmers interplant maize and sorghum in a variety of geometric and nongeometric patterns.

Four stress treatments were applied to the systems. In both Year 1 and 2 half the leaves were systematically removed from the site from all species in the defoliation treatment. In Year 2 resource levels were increased by fertilization and watering treatments; losses to herbivores were reduced in a pesticide-sprayed treatment. The "control" treatment was managed with typical local methods (periodic hand weeding and no fossil fuel inputs).

Table 4. Planting proportions, densities, and spacings in the experimental systems.

SYSTEM	CROP	PROPORTION OF FULL STAND	DENSITY (no./ha)	SPACING (cm)
MAIZE	MAIZE	1	44,444	90 x 25
SPARSE MAIZE	MAIZE	1/2	22,222	90 x 50
SORGHUM	SORGHUM	1	111,111	60 x 15
COWPEA	COWPEA	1	66,667	75 x 20
PUMPKIN	PUMPKIN	1	13,889	120 x 120[a]
MAIZE-SORGHUM	MAIZE	1/2	22,222	180 x 25
	SORGHUM	1/2	55,556	90 x 20
	TOTAL	1	77,778	
MAIZE-COWPEA	MAIZE	1/2	22,222	90 x 50
	COWPEA	1/2 (.48)	31,746	90 x 35
	TOTAL	1 (.98)	53,968	
MAIZE-PUMPKIN	MAIZE	2/3	29,630	90 x 37.5
	PUMPKIN	1/3	4,630	240 x 180[a]
	TOTAL	1	34,260	
FOUR-CROP	MAIZE	1/4	11,111	180 x 50
	SORGHUM	1/4	27,778	180 x 20
	COWPEA	1/4 (.23)	15,385	90 x 65[b]
	PUMPKIN	1/4	3,419	325 x 180[a]
	TOTAL	1 (.98)	57,693	

[a]two plants per hole

[b]every fifth hole in every other row planted to pumpkin, not cowpea

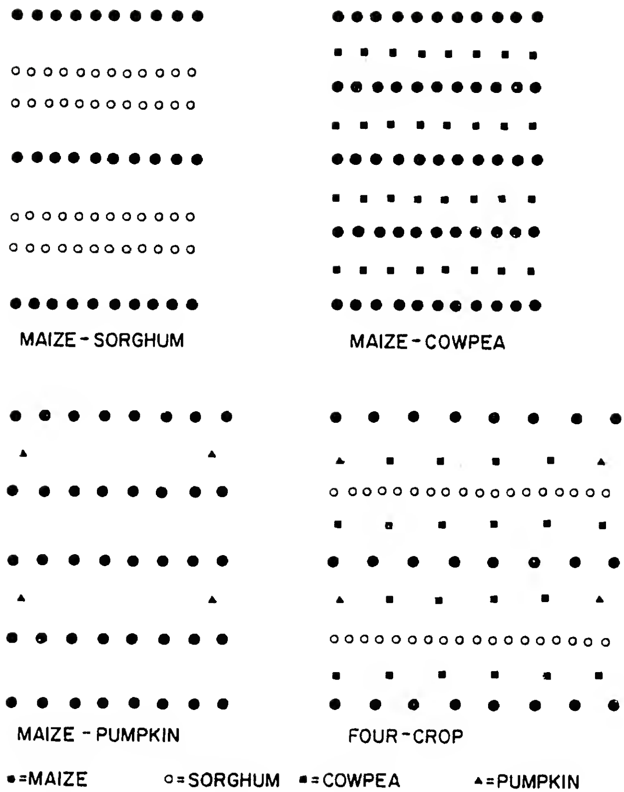

Figure 2. Intercrop planting patterns. Inter-row distance of maize is 90 cm in the maize-cowpea and maize-pumpkin intercrops, and 180 cm in the maize-sorghum and four-crop intercrops; other distances are to scale.

Plot Layout

In both years a rectangular array of plots was constructed, then systems and/or treatments were randomly assigned to the array. In Year 1, two separate experiments were conducted (Figure 3). In the main experiment, the 11 experimental systems were compared in the "control" treatment only (farmer's conditions). Three replicates per system, a total of 33, 15 x 21 m plots, were separated by 2 m walkways. A 2 m buffer strip within each plot surrounded the sampling area, which was divided into 6, 5 x 5 m subplots with 1 m walkways between for easier management. In the second experiment, response to defoliation was investigated in an adjacent set of 60, 8 x 10 m plots (2 treatments x 10 systems x 3 replicates). These plots were also separated by 2 m walkways and contained 2 m buffer strips surrounding 4 x 6 m sampling areas.

Results from Year 1 suggested several changes in design for Year 2. Due to extremely high plot-to-plot variability, more replicates of smaller plot size were planted. In addition, the three two-crop systems, sparse maize, and the bare ground system were eliminated to allow greater experimentation with stress treatments. The stress treatments and main plots were combined into a single experiment in Year 2, shown in Figure 3. All plots were 8 x 10 m, separated by 1 m walkways and containing 1 m buffer strips around 6 x 8 m sampling areas. The watering and pesticide treatments were isolated in blocks separated by 3 m walkways from the other three treatments to avoid contamination. The watering treatment was located in the southeast corner of the site, near the water source, and pesticide plots were located along the

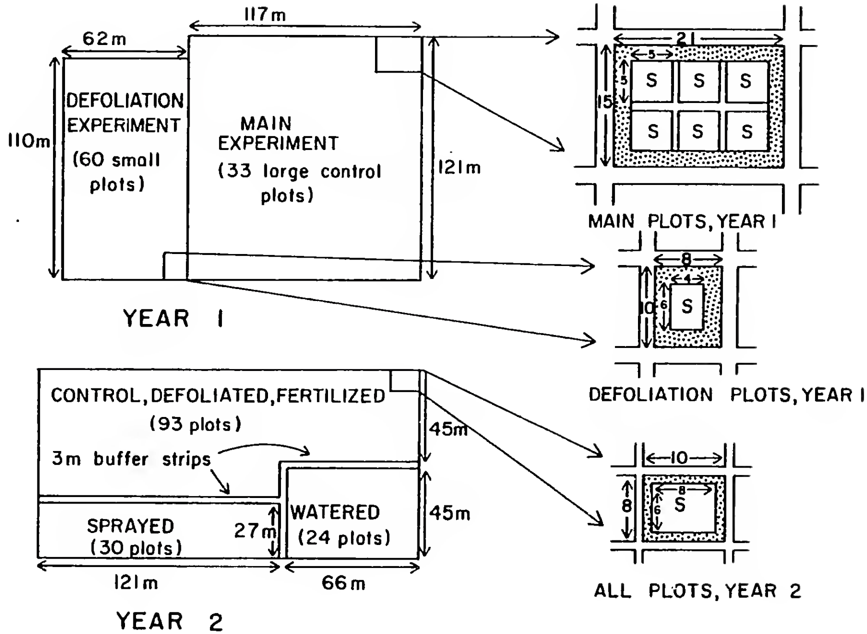

Figure 3. Field plot layout, Years 1 and 2. S = sampling area; dotted area = buffer strip of the experimental system; clear area = walkway.

south edge. (Daytime wind direction was unpredictable.) Plots of the six experimental systems were randomly assigned within each of these two treatments, and plots for the other three treatments were randomly assigned to the remaining area. To save labor and increase replication of the control plots, watered plots were replicated only four times (24 plots total), control treatment plots six times. The other three treatments were replicated five times per system. Two plots were eliminated due to standing water on the entire plot, and three due to planting or treatment errors. Plots covered incompletely or briefly with standing water were not eliminated. No system-by-treatment combination contained fewer than four replicates.

Plot Management

Agronomic Management

The chronology of various agronomic and experimental activities in Years 1 and 2 is shown in Figure 4. Weekly rainfall is given as a corresponding histogram. Each cultural operation (planting, thinning, weeding, harvesting) took a maximum of six days to complete (usually fewer than four). To minimize age differences, operations were conducted systematically throughout the field, going up one row of plots and down the next, following the original planting order. The succession system was slightly older than the crop systems due to natural seeding, and a correction for this was applied in the results where possible.

In Year 1 the land was plowed and harrowed just before planting. Judging from the survey of farmers, this was a common practice, and

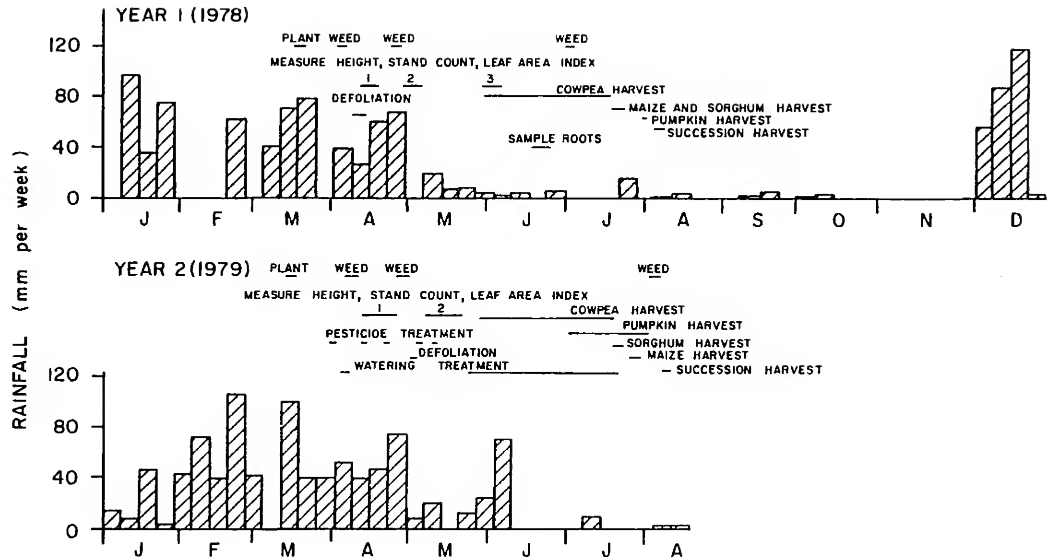

Figure 4. Distribution of rainfall and agronomic activities, Years 1 and 2.

was almost a necessity in view of the time requirements and expense of hand-clearing fallow land. In Year 2 the land was too wet to plow during the last two weeks of February, and finally a crew of 40 workers hand-cultivated the site in time for planting in mid-March. In both years the ground was cleared of weedy residue by hand and quickly surface-hoed a second time to make a smooth surface for planting.

The middle day of planting (March 18 in Year 1, March 12 in Year 2) was designated day 0; planting took five days in Year 1, 3 in Year 2. Between-row and within-row planting distances were measured with marked ropes. Using the traditional dibble-stick method, maize (variety Ilonga Composite) was planted 3 seeds/hole; sorghum (Serena), 5 seeds/hole; cowpea (a nonclimbing SVS3 variety), 3 seeds/hole; and pumpkin (local variety), 4 seeds/hole. Good germination occurred in both years, but a few seedlings were transplanted when 5-10 cm high to fill gaps and achieve the desired planting density. The stands were thinned at two to three weeks to one plant per hole for all species except pumpkin (two per hole). All systems except natural succession were weeded three times, as necessary, in both years. The third weeding was used to monitor weed growth and was not necessary from an agronomic standpoint. Cowpea pods did not mature synchronously and were harvested several times over the period shown in Figure 4. Pumpkins were also continuously harvested, but all other crops were harvested only once. All aboveground biomass was harvested and separated into edible and nonedible components.

Application of Stress Treatments

On the fertilizer-treated plots, P_2O_5 from triple super phosphate was hoed into shallow furrows along the rows or (for pumpkin only) holes at planting, at the rate of 40 kg/ha. Nitrogen was applied as a top-dressing along the rows at day 28 at the rate of 40 kg/ha as 200 kg/ha ammonium sulfate, the most commonly used and available nitrogen fertilizer. In successional plots, fertilizer was applied along imaginary rows 90 cm apart. Fertilization rates were those recommended by the Soil Science Department in Morogoro for local conditions.

Plots designated for the watering treatment were in fact not watered much, due to abundant rainfall during most of the growing season. Seedlings were watered once after emergence (day 21) and from day 63 until harvest. Water was applied directly to the plant bases using a hose. Successional plants were watered by standing outside the sampling area as much as possible, inserting the hose into the vegetation layer, and letting it run for several minutes before moving it to the next point 1-2 m away.

Plots designated for defoliation were cut on day 20-25 (Year 1) and day 49-50 (Year 2) and the cuttings removed from the plots. The delay in Year 2 was due to the later first weeding, creating a labor shortage during the hectic third through seventh weeks. Whenever possible, every other leaf was cut where it joined the stem. This system worked well for maize, sorghum, and pumpkin, but was difficult in cowpeas due to the high degree of branching and in succession because of the density of stems. Instead, in cowpeas, all leaves on one side of the plant (partitioned by an imaginary line along the row) were taken.

In the successional plots, all biomass above 15 cm (Year 1) and 20 cm (Year 2) was removed. This represented approximately 71 percent of successional leaf area in Year 1 (estimated from the first LAI measurement) and 57 percent of successional LAI in Year 2 (estimated from the second LAI measurement and linearly interpolated by height). While the cowpea and succession defoliation methods do not imitate natural leaf-removing processes as well as the alternate-leaf method, they could be used reliably by workers with minimal additional damage to the vegetation by stem breakage.

The "pesticide" treatment was intended to reduce but not to completely eliminate pest populations in a regime a farmer might conceivably use. Spraying was stopped more than two weeks before the harvest to avoid contamination. Sixty percent diazinon was selected as a broad spectrum organo-phosphate pesticide effective against most groups of insect pests. The pesticide-treated plots were sprayed five times with diazinon at approximately ten-day intervals, beginning day 17 (Figure 4). Application rate was 2.2 liters emulsifiable concentrate/ha (recommended rate is 0.4-3.5 liters/ha). The second diazinon spraying was mixed with the rainfast fungicide Blitox (50 percent copper oxychloride) at an application rate of 1 kg/ha. The mixture caused moderate leaf damage to maize and sorghum, and was clearly phytotoxic to pumpkin. Finally, as systematic protection against sap feeders and stem borers during crop maturation, dimecron (phosphamidon) was sprayed at approximately 300 g active ingredient/ha on day 58.

Measures of System and Species Response

The response variables may be conceptualized as falling into four groups: growth and productivity, resource use, resistance to natural stressors, and response to artificial stress augmentation or amelioration. These groups are not entirely exclusive; one variable may contribute information in two or more of these categories.

Sampling regimes for the variables measured are described below. Sampling took four or fewer days except where noted (the days given are mid-days of the sampling periods). Systematic, rather than random, sampling was frequently used to save time. Systematic samples were taken such that individuals were selected from all locations in all plots; sample size varied somewhat to meet this condition. The first individual to be sampled in each row or plot was chosen randomly, and the interval between individuals did not correspond to any regularity in the planting patterns. For example, in the four-crop system cowpeas were not sampled at an interval of four, since this is the interval at which pumpkins were interplanted.

Growth and Productivity

The term productivity is used here in the broad sense of biomass accumulation per unit time (one growing season), and not in the usual sense of net primary productivity (NPP). Net primary productivity is rarely measured, and would theoretically include biomass that dies, drops off the plant, decomposes, or is consumed by herbivores. Turnover of plant parts was not measured in this study because of the short growing period involved and high rate of biomass accumulation of the

systems being studied, and because the primary purpose of the study was to make comparisons among systems rather than to determine NPP. In mature ecosystems, changes in standing biomass may be unsatisfactory indicators of net productivity because of high rates of death, decomposition, and consumption. For agricultural and early successional systems, however, where biomass accumulates rapidly, changes in standing crop of biomass, leaves, roots, etc., should be reasonably reliable measures of productivity. Accumulation of edible biomass is an important system attribute in its own right. Throughout the presentation and discussion of the results of this study, the unit of time over which growth or biomass accretion was measured is either given or assumed to be the entire growing season (final harvest data).

Total and edible biomass

Total and edible biomass production, perhaps the best indicators of species and system performance, were determined at harvest. All crops were harvested at their appropriate time rather than synchronously. Cowpea pods were harvested three times, pumpkins were harvested as they ripened, and maize and sorghum were harvested nearly synchronously (Figure 4). Natural succession plots were harvested after the cropping systems.

Although some systems (e.g., cowpea) matured slightly before others, all systems essentially filled the main growing season. Therefore, all parameters related to yield are implicitly expressed as production per growing season, rather than per day or per month. Changing the time unit might affect tests of differences among systems but

should not influence comparisions of a given species' performance among systems or differences between intercrops and corresponding monocultures.

All aboveground biomass, including dead material lying on the ground and/or attached to the plants, was collected, divided into various components, subsampled if necessary, dried at 80°C, and weighed. Edible and total aboveground yield per area, and edible and total yield per plant were calculated. Edible yield from the succession plots was assumed to be zero, and per-plant calculations were not performed for the succession system. Total biomass at harvest of defoliated plots did not include the biomass of defoliated leaves unless specified. Allocation ratio was calculated as (edible biomass)/(total aboveground biomass).

Biomass at physiological maturity (flowering)

In Year 2, subplots of all systems in the control and fertilized treatments were harvested approximately at flowering (day 52, cowpea; day 71, succession; day 73, sorghum; day 77, maize; day 79, pumpkin). Plants in a 12 m^2 (agronomic systems) or 6 m^2 (successional system) area were harvested by hoe, including roots to a depth of approximately 15 cm. In the successional system, monocots and dicots were separated; the roots cut off at soil level; and the roots and shoots washed, air dried, subsampled, ovendried at 80°C, and weighed. Maize plants were divided into leaves, stems, tassels, ears, and roots; sorghum into leaves, stems, panicles, and roots; cowpeas into leaves, stems, pods, and roots; and pumpkin into leaves, stems, flowers, fruits, roots, and shoots. Each category was washed, subsampled, dried, and weighed.

Moisture content of the subsamples of each category was averaged for each system-by-treatment combination. Root/shoot ratios were calculated for the four agronomic species, successional monocots, and successional dicots.

Leaf mass at defoliation

The mass of defoliated leaves represents one-half the standing crop of leaves at the time of defoliation, and was used to compare leaf production up to the time of defoliation, and to calculate a measure of total biomass production that included cut leaves. Defoliated leaves of each species were collected, subsampled if necessary, dried at 80°C, and weighed.

Miscellaneous productivity measures

In addition to the basic productivity measures, other measures of yield or biomass distribution were derived from the harvest data, which included counts of cowpea seeds and pods, maize cobs, sorghum panicles, and pumpkin fruits. For cowpeas, these measures were percent edible seeds (by mass, Years 1 and 2), percent edible seeds (by number, Year 1 and 2), number of pods per plant (Year 1), number of seeds per pod (Year 1), and number of edible seeds per pod (Year 1). For sorghum, the additional yield parameters were number of heads per plant (all plots, Year 2) and percent of heads with greater than 75 percent of the head surface area filled with grain (all plots, Year 2). Tillering was also monitored in sorghum. Number of maize cobs per plant and maize grain yield per cob were determined for all plots in Year 1;

number of pumpkin fruits per plant and edible yield per pumpkin fruit were determined for all plots in Year 2.

LAI and canopy cover

Leaf Area Index (LAI) and canopy cover are measures of leaf production as well as a species' or system's potential to capture light (discussed in the section on resource use, below). Leaf Area Index was measured by the "plumb-bob" method using a fishing rod and reel apparatus (Benedict 1976) to lower a weighted string vertically through the canopy. The number of leaves hitting the string, averaged over a number of trials at different points, equals LAI. This method underestimates actual leaf surface area because leaves oriented vertically are less likely to be touched by the string than horizontal leaves of the same area. This error may be rather significant when comparing LAI of different systems on an absolute basis, but should not be important when comparing a given species' LAI among systems or LAI of intercrops and corresponding monocultures.

Leaf Area Index was measured in control-treatment plots on days 28, 46, and 74 in Year 1 and in control, fertilized, and pesticide-sprayed plots on days 40 and 65 in Year 2. Samples were not taken in wet or windy weather; each sample took two people a maximum of seven days to complete. Sixty measurements were made on each plot: six at each of 10 random points located at least 2 m from each other and 1 m from the edge of the sampling area. The average LAI from the 60 points was treated as a single replicate in the analysis. Height by 15 cm intervals and by the species of each leaf the line touched was

recorded in all systems except succession, where only plant class (monocot or dicot) was noted. Since successional vegetation had a "head start" on the crop systems, the LAI of the successional system was set back seven days on each sampling date by linear interpolation. The "system LAI" of an intercrop system is the sum of the LAIs of its component species. Canopy cover was calculated as the percent of trials (of the 60 per plot) in which one or more leaves was hit. Canopy cover is a system-level variable; ground cover by species was not calculated.

Cowpea third-leaf area

A measure related to cowpea LAI, the area of the third leaf up from the cotyledon, was obtained as part of herbivory measurements on day 22 (Year 1) and day 30 (Year 2). The sampling and area measurement techniques are given in the section on cowpea leaf herbivory, below.

Specific leaf mass

Specific leaf mass (g/m^2 leaf) was determined on day 71, Year 2. Leaves of three systematically selected plants of each crop species were harvested from the border strips of each plot, the leaf area determined, and the samples dried at 80°C and weighed to determine mass per unit leaf area. In the successional system, specific leaf mass of monocots and dicots was determined for a composite sample of three systematically-selected, approximately 10-cm-diameter samples of vegetation from the border strip of each plot. Leaf Area Index of the crop species was calculated as leaf biomass divided by specific leaf

mass. Biomass of leaves and stems was not separated in the successional plots,so LAI could not be determined.

Root biomass

In Year 1, root biomass was determined by taking soil cores to a depth of 40 cm with an 8 cm diameter root auger on day 96. The cores were taken in 10 cm depth intervals and the soil carefully rinsed off each segment of each core through approximately 12 strand/cm screens. The roots were then dried at 80°C and weighed to 10^{-4} g. Living and dead roots, and roots of different species, could not be differentiated. Root biomass data were corrected for roots remaining from the previous fallow by subtracting (by depth interval) root biomass determined on the bare ground plots.

Root cores were taken along a line perpendicular to planting rows, at a systematic interval that did not correspond to the inter-row distance. It was felt that this gave a more representative sample than would coring at random points, in view of the very limited sample size. Ten cores were taken from two plots in the maize-sorghum and maize-cowpea systems, five cores from one plot in each of the other nine systems.

Roots were also sampled by a complete harvest method at flowering in Year 2 (see above). Year 2 values were not corrected for residual roots because the previous vegetation (the Year 1 experiment) was less than one year old and residual roots were few at the start of the Year 2 growing season.

Root biomass was used as an indicator of root activity in this study. Root surface area may be a better measure because large roots are not active in proportion to their biomass; all systems in this study were of equal and low age, however, and large roots were absent.

Stem length

Height or length of individuals of each crop species was measured on days 28, 46, and 89 (Year 1) and days 36 and 59 (Year 2). Control plots (Year 1) and plots of all treatments (Year 2) were sampled. Systematic samples were taken in each system, ranging from every 15th plant in every other row (sorghum monoculture) to every plant (pumpkin in four-crop system). Sample size was 39-51 in Year 1 and 13-32 in Year 2 (except pumpkin, n = 1-30). Maize and sorghum plants were measured from the soil surface to the straightened tip of the longest leaf; cowpea was measured along the primary stem to the main meristem; pumpkin was measured along its longest branch to the farthest meristem.

Survivorship

Survivorship was calculated from stand counts taken on days 24, 53, and 74 (Year 1) and days 28, 56, and 96 (Year 2). In Year 1, the subplots of each main plot were surveyed and the results summed; in Year 2 the 6 x 8 m sampling areas of all plots were inventoried. Natural successional vegetation was not inventoried due to the difficulty of distinguishing individuals. Mortality/30 days was calculated from survivorship for the intervals between samples and for the growing season as a whole. Stand counts were also converted to percent of full stand (recommended or target planting density). At the first sampling date, percent full stand ("fullstandedness") gives a measure of how well the desired planting density was achieved (success of crop establishment). For later sampling dates, fullstandedness of species in a system can be summed to give a measure of plant survival on a system level, a property I called "system fullstandedness." If

no mortality occurred, system fullstandedness would be one in all systems except sparse maize, where it should be 0.5.

Resource Use

Ability of the experimental systems to exploit available resources was of interest as a possible explanation for differences in productivity. While it was difficult in most cases to obtain direct measures of resource utilization, several collateral measures that should be correlated with use of certain resources were obtained.

LAI

Amount and vertical distribution of LAI were used as indicators of light interception in the experimental systems. Sampling methods are given above.

Root biomass

Amount and distribution of root biomass are indicators of utilization of the soil volume and soil resources (primarily, water and nutrients). Profiles of root biomass in 10-cm intervals from 0-40 cm depth were constructed for all systesm in Year 1, as described above.

Soil moisture

Soil moisture was monitored by gravimetric methods in Year 2. A tube-type soil auger was used to collect soil samples every two to three days from the 15-30 cm depth zone. The samples were plastic-bagged in the field, weighed, dried at 80°C, reweighed, and the moisture content calculated as (wet weight-dry weight)/(dry weight). Each day's samples

were taken from random points in a random selection of 25 plots; these were later grouped into ten-day intervals to allow sufficient replication by system and treatment to perform analysis of variance for each interval.

Labor

A resource that is not usually monitored but is very important to small farmers is labor. It was evident from the interviews that human labor often limits the area planted. In Year 1, planting labor was measured for the 60 small control and defoliation plots and weeding labor was measured in the 33 main control plots, for the first and second weedings. In Year 2, planting labor and first and second weeding labor were measured in all plots. Crews of five to seven workers were timed to the nearest five seconds and this was converted to person-hours/ha. Since planting time included time to align and hold ropes and to plant at the proper marked intervals, these determinations of planting labor almost certainly overestimate the labor a small farmer would use. The same is true of weeding labor, since it included thoroughly cleaning the ground of weeds and collecting them for weighing. The measures are nevertheless useful for comparative purposes. Efficiency of labor use was also calculated, as the ratio of edible and total biomass output to labor input.

Resistance to Natural Stressors

Stressors provided by nature were used to test hypotheses about the resistance of the experimental systems to energy drains. All of the growth and productivity measures in control plots reflect the

species' and systems' reaction to the sum of all naturally occurring stressors, and are therefore included in this category. In addition, the impact of a number of specific natural stressors was monitored, including weed growth; lodging in windstorms; and population levels of various pests and diseases, usually measured in terms of frequency of affected host plants.

Weed growth

Competition by weeds is especially important to small farmers, who often do not weed their fields as often or as thoroughly as was done in this study. Weeds were hoed, collected, trimmed of roots, subsampled, dried at 80°C, and weighed. Samples were taken from control plots in the first, second, and third weedings in Year 1 (days 17, 39 and 78) and from control, fertilized, and watered plots in the second and third weedings in Year 2 (days 44 and 107). The first weed sample in Year 2 was discarded due to a sampling error.

Lodging

In both years a windstorm occurred as the crops were approaching maturity, conveniently providing an opportunity to measure susceptibility to lodging. The number of maize and sorghum plants inclined at greater than 45° from vertical was recorded for all control plots on day 76 in Year 1, and for control and defoliated plots on day 74, Year 2. No measure could be devised that would meaningfully compare the degree of lodging in maize and sorghum with that in the other experimental systems.

Pests and diseases

The surveys conducted were intended to be representative, rather than exhaustive, of the important pests and diseases, and were limited by time, the need to isolate and identify pests, and constraints on destructive sampling. In some cases, non-pest-specific plant symptoms (e.g., leaf discoloration) were used as variables due to the difficulty of separating and identifying the multiple causes of those symptoms. Monitoring methods are described below by crop. Most pest and disease levels are expressed as percent of plants, leaves, pods, or other plant part affected.

Rat holes. Shortly after planting, rats excavated some of the planting holes, eating the seeds. The number of rat holes per plot was counted in the 60 small control and defoliated plots on approximately day 4, Year 1, for possible correlation with crop system.

Maize streak virus. Maize streak is a viral disease carried by the maize leafhopper *Cicadulina mbila* (Homoptera: Cicadellidae), and is easily identified by broken white lines parallel to the leaf veins. Systematic samples of maize plants were scored by degree of infection: 0 (no symptoms), 1 (five or fewer leaves with symptoms), or 2 (more than five leaves with symptoms). From 91-367 plants were scored in each control plot on day 31 of Year 1. From 27-91 plants were sampled on all plots on day 34, and 17-59 plants per plot on day 80, in Year 2. The data were later reduced to percent of plants having any symptoms.

Maize stalk borer. The maize stalk borer *Busseola fusca* (Lepidoptera: Noctuidae) completes one generation in the stem of the growing maize plant and a second generation in the cobs and stems of

maturing plants and trash left on the field after harvest. Populations of stalk borers were counted in systematic samples of 100 seedlings per plot on day 13 in Year 2 by counting the number with "windowing," characteristic strips of holes in leaves that result from borers entering the stem.

Sorghum shoot fly and tillering. Maggots of the sorghum shoot fly Atherigona indica (Diptera: Muscidae) bore into young sorghum shoots, causing death of the main shoot ("dead heart") and a compensatory sprouting of new side shoots (tillering). Systematic samples of 380-676 plants were monitored for dead heart in control plots on day 32, Year 1, and complete samples of 104-533 plants were taken during the day 22 stand count for all plots in Year 2. Percent of plants tillering was also measured on day 47, Year 1 (50 systematically selected individuals per control plot) and on day 57 in Year 2 (complete samples of 105-512 plants in each plot, measured in plots of all treatments).

Sorghum stalk borer. Sorghum stalk borers, primarily Busseola fusca but possibly some individuals of Chilo and Sesamia species also, were counted at harvest on day 130 in Year 2. Systematic samples of 25 main stems per plot were scored by number of borer exit holes. These data were later reduced to percent of stems having any exit holes.

Striga. Striga hermontheca and Striga asiatica (Scrophulariaceae) are plant parasites that attach to and feed on roots of maize and sorghum. The Striga individuals were counted in all maize and sorghum plots on day 77, Year 1, and the data expressed as individuals per unit area.

Pumpkin melonfly. The pumpkin melonfly Dacus cucurbitae (Diptera: Trypetidae) oviposits under the skin of developing pumpkin fruits, where

the larvae cause the fruit to partially or totally discolor and in extreme cases to rot and fall off the vine. Melonfly damage was assessed for all fruits in control plots on approximately day 70, Year 1, and in all plots on day 80, Year 2. Data from plots having fewer than five fruits were deleted. Fruits were scored by degree of melonfly attack: 0 (no visible damage), 1 (one or more entry holes visible), or 2 (fruit discolored or fallen off the vine). These data were later reduced to percent of fruits having any visible damage.

Pumpkin leaf discoloration. Pumpkin leaves are susceptible to a number of leaf diseases, of which powdery mildew (*Erysiphe cichoracearum*), downy mildew (*Pseudoperonospora cubensis*) and an unidentified mosaic virus were present on the experimental pumpkin plants. (Other diseases may also have been present.) Rather than attempt to differentiate the symptoms of these diseases, percent of leaves with any kind of leaf discoloration was measured. Leaf miner trails, discoloration around holes, etc., were not included, so the discoloration variable should reflect the status of the plant with respect to leaf diseases in general. A systematic sample of 44-56 pumpkin plants was surveyed in each control plot on day 76, Year 1. Each plant was scored according to the number of leaves that were partially or totally discolored: 0 (none discolored), 1 (five or fewer leaves discolored), or 2 (more than five leaves discolored). These data were later reduced to percent of plants with more than five leaves discolored.

Cowpea leaf herbivory. Young cowpea plants were heavily infested with the beetle *Ootheca bennigseni*, causing considerable loss of leaf area through herbivory. Leaf area loss was determined for systematic

samples of 43-71 leaves per plot (day 22, Year 1) and 10-17 leaves per plot (day 30, Year 2). Only the third leaf up from the cotyledon was sampled for each plant since the object was to make comparisons among systems rather than to measure total leaf consumption. No correlation was made for leaf expansion because the data were to be used to compare herbivory on fully expanded leaves of like ages. Total leaf area (area if herbivory had been zero) was determined by tracing the leaves on opaque paper, approximating the original margins where missing, cutting out the traces, and measuring their area on a leaf area meter. Area of tracings were adjusted downward by 8.7 percent to correct for error during tracing and cutting, as determined by a sample of 55 uneaten leaves and their paper counterparts. The "residual area," or leaf area remaining after herbivory, was determined by measuring the leaves themselves in the area meter. To improve accuracy since the meter had a faulty 0.1 cm^2 display, the leaf samples from each plot were measured as a group. Control plots were sampled in Year 1, all plots in Year 2.

Cowpea aphids. Percent of cowpea plants on which *Aphis fabae* (Homoptera: Aphididae) were found was measured in control plots on day 88, Year 1 and in all plots on day 80, Year 2. The samples contained 23-121 (Year 1) and 28-122 (Year 2) systematically selected plants.

Cowpea leaf diseases. Three cowpea leaf diseases could be distinguished well enough to be reliably scored. Top necrosis, a common viral disease in the Morogoro area, causes characteristic yellow mottling and leaf shrivelling very similar to that caused by cowpea mosaic virus. Occurrence of top necrosis was recorded for systematic samples of 139-349 plants for control plots on day 39,

Year 1, and 28-71 plants for all plots on day 53, Year 2. Three degrees of severity of top necrosis were recorded: 0 (no symptoms), 1 (fewer than five leaves with symptoms), and 2 (five or more leaves with symptoms). These data were later reduced to percent of plants having any symptoms of top necrosis.

The pseudorust Synchitrium dolichi produced obvious orange patches on leaves and stems, and powdery mildew (Erysiphe polygoni) created easily distinguished white patches on leaves. Presence or absence of these two diseases was recorded in the same sample in which aphids were counted (above).

Cowpea seed and pod discoloration. Many cowpea seeds and pods were disformed and discolored as a result of numerous pests and diseases. Discoloration seemed to be primarily caused by unidentified fungal diseases but may also have been caused to some extent by heteropteran feeding. Pod discoloration was scored as 0 (no discoloration), 1 (less than 25 percent of the pod surface discolored), or 2 (more than 25 percent of the pod surface discolored) for random samples of 59-120 pods per plot from the first harvest in control plots, Year 1, and 5-20 pods per plot from the three harvests from all plots, Year 2. Most samples contained the maximum number of pods in this range; occasional smaller samples were from low-yielding plots, where all pods were sampled. The data were later reduced to percent of pods having any fungal discoloration. In Year 2, a three-harvest average was calculated by weighting percent discolored pods by pod mass for the three harvests.

A distinctive oval, off-white growth on the pods thought to be a scab disease was also monitored in Year 2 in the same pod samples

that were scored for pod discoloration. Percent of scab-infected pods was determined for all three harvests and the weighted average calculated as above.

Cowpea seeds were inspected for several types of damage, including seed discoloration, in samples from the first harvest of control plots (Year 1) and all three harvests from all plots (Year 2). Seeds were scored as discolored or not discolored; browning around the edges of holes was not included. In Year 1 a small cup was used to remove a random sample of seeds from each subplot's well-mixed bag of seed yield. In Year 2 all seeds were sampled. Sample size ranged from 648-865 (sum of six subplots) in Year 1 and from 0-1196 in Year 2. In Year 2, a three-harvest average was calculated by weighting the percent of discolored seeds by the number of seeds in each harvest.

Cowpea Maruca damage. *Maruca testiculatis* (Lepidoptera) larvae feed on cowpea flowers and seeds, causing considerable yield reduction. The population of *Maruca* larvae in closed cowpea flowers was sampled on day 81, Year 2. Presence or absence of larvae was scored in 1-40 flowers from the border strips surrounding the sampling areas of cowpea plots. Samples containing fewer than five flowers were later discarded. In addition, percent of pods having one or more *Maruca* exit holes was recorded and the three-harvest average calculated for the pod samples described above. Percent of seeds partially eaten by *Maruca* larvae was also recorded and the three-harvest average calculated for the seed samples described above.

Other cowpea seed damage. Seed shrivelling and seed bruchid beetle holes were recorded and the three-harvest average calculated for

the seed samples. In addition, the percent of seeds without any visible damage was recorded as a composite measure of susceptibility to pests and diseases. Shrivelling or wrinkling of seeds was due primarily to piercing-sucking feeding by Acanthomia horrida but may also be attributable in part to thrips. Acanthoscelides obtectus (Coleoptera: Bruchidae) produced small holes or characteristic transparent "windows" in the seed coat that could be easily distinguished and counted.

Methods of Analysis

Some of the above response measures are related to whole-system function, while others pertain to a given species' performance. For convenience, successional monocots and successional dicots as well as the four crop species are referred to as "species." Some parameters, such as LAI and yield, were measured both on the species and system level.

Three Types of Analysis

Three general types of analysis were performed: (1) absolute comparisions of system performance (system-level measures only), (2) comparisons of intercrop performance with that of a weighted mean of corresponding monocultures (system-level measures), and (3) comparison of each species' performance in intercrop and monoculture systems.

Absolute comparision of system performance

The response measures were compared among systems and treatments by analysis of variance (ANOVA). The measures were not adjusted for

planting density. This type of analysis tests for absolute differences among systems and treatments, without regard for crop composition or planting density.

Comparison of intercrops and corresponding monocultures

Whole-system performance of the intercrops was compared with a weighted mean of corresponding monocultures by the Contrast procedure of the Statistical Analysis System (SAS) statistical computer program package (Helwig 1978). In this procedure, the given variable is compared with several other variables that are weighted as specified. The weighting factors were the fractions of the intercrop system allocated to each species. Thus, system LAI of the maize-sorghum intercrop could be compared with maize and sorghum LAI's, weighted equally. In the maize-cowpea system the weighting factors were also 1/2 + 1/2; in maize-pumpkin, 2/3 + 1/3; and in the four-crop system, 1/4 + 1/4 + 1/4 + 1/4. Intercrop performance was also compared with that of corresponding monocultures using Yield Equivalent Ratio (YER).

Comparison of species performance in intercrops and monocultures

Measures of species performance (e.g., sorghum LAI) were corrected for planting density, creating a new variable ("adjusted sorghum LAI") on which the ANOVA was performed. In this example, adjusted sorghum LAI equals sorghum LAI x 2 for the maize-sorghum system, and sorghum LAI x 4 for the four-crop system. Adjusted variables equal the unadjusted value for the monoculture systems (and successional monocots and dicots). Analyses of variance performed on density-adjusted species variables test for differences in a species' performance in different systems or

treatments, and are roughly equivalent to testing for differences in per-plant performance. Variables expressed as frequencies were not adjusted for planting density. Species performance was also evaluated by the species' Yield Equivalent Ratio (YER), the ratio of a species' yield in intercrop to its expected yield based on planting density and monoculture yield.

Analyses of Variance

Data from the three experimental data sets (Year 1 main control plots; Year 1 small control and defoliated plots; Year 2 plots of all treatments) were analyzed separately due to inherent differences including plot size, weather, and sampling dates. One-way ANOVA by system was performed on the data from the main control plots, Year 1, and two-way ANOVA by system and treatment for the other two data sets.

Equality of variance among groups being compared is one of the assumptions of ANOVA. Levene's test, in Biomedical Data Programs program P7D (Dixon and Brown 1979) was used to test this assumption for each variable. Species variables were tested for equality of variance both before and after adjustment for planting density. Normality was not tested for because ANOVA is known to be relatively insensitive to deviations from this assumption (Sokal and Rohlf 1969, Steele and Torrie 1980).

Almost all variables met the equal variance assumption as tested by the BMDP program. This may have been due partly to small sample size and partly to the fact that many variables were taken as means, and should therefore be normally distributed with reduced variances.

Four variables had unequal variance ($p < .05$): system edible yield (Year 2), system total yield (Year 2), pumpkin edible yield (Year 2), and adjusted pumpkin edible yield (Year 2). Log transformation would be expected to reduce variance inequality due to differences in growth rate of difference species, but log transformation did not equalize the variance of the above variables (except adjusted pumpkin edible yield, and that because the program eliminated variances of zero, from the four-crop system, from the calculation). On closer inspection it was evident that the unequal variance of all four variables was due to great fluctuation in pumpkin edible and total yield in the pumpkin monoculture plots. I ignored this relatively minor departure from the ANOVA assumptions, and did not transform any of the response variables.

The spatial isolation of the watered and pesticide-sprayed plots in Year 2 raises the question of whether the ANOVA assumption of randomness was seriously violated. This was unlikely since all plots were located within approximately 250 m of each other, and soil analysis had revealed no clear trends in soil pH or nutrients across the site. As a further check the test of equality of variance was performed on all variables without the water and pesticide plots, and little or no improvement in variance equality resulted. Plot-to-plot variability by system and treatment was no greater when water and pesticide plots were included than when they were omitted.

The ANOVA was conducted with the General Linear Model (GLM) procedure of the SAS package, due to unequal replication, followed by the Duncan procedure (Duncan's multiple range test) to detect specific differences among systems and treatments. In two-way ANOVAs where system-by-treatment interaction was significant, Duncan's tests of system

differences were performed for each system. When system-by-treatment interaction was nonsignificant, tests for differences among systems were performed on data from plots of all treatments, and tests for differences among treatments were performed on data from plots of all systems. In the figures, the composition of the data sets or "samples" on which the Duncan's tests were performed is described where any ambiguity exists. A significance level of $p < .05$ was used throughout the analyses unless otherwise specified.

In many cases, striking differences in mean levels of response variables were not found to be statistically significant by the ANOVA and Duncan's tests. This was especially true of differences among systems in Year 1, where the number of systems was high and the number of replicates low. Duncan's tests performed by system or treatment tended to give lower significance than those performed for all systems or treatments combined, due to reduced sample size. In interpretation of results, therefore, some weight has been given to consistency of trends (among several variables, across treatments, and in the two study years) as well as the results of the statistical tests.

Analysis of Stability

Several approaches were taken to assess the stability of the experimental systems and the species comprising them. Levels of naturally occurring stressors were measured (e.g., pest frequencies) and system comparisons made by ANOVA. Pest levels were also correlated with productivity; strong negative correlations suggest that either high productivity reduces pest levels or pests reduce productivity. The effects of the pesticide treatment on both pest levels and productivity indirectly indicate

the importance of pests as productivity drains in the agricultural systems studied.

The second measure of stability was the productivity change of the systems and their component species in the fertilization, pesticide, defoliation, and watering treatments. Both absolute magnitude of change and percent change from controls were calculated; absolute change is here called "response," and percent change is called "responsiveness." The sign of the change is ignored. Differing system responses to change in stress level indicate differences in resource use. Responsiveness is a measure of instability; those systems or species least responsive to changes in levels of stressors should also be the most constant. Responsiveness of species to increases in diversity (reduced competition stress) was also used as a measure of species stability.

Finally, the coefficient of variation (standard deviation/mean) of systems or species over the range of stress treatments was determined as a measure of overall constancy. Year 1 and Year 2 data were not combined for this measure due to differing plot size. Temporal (year-to-year) variability was also assessed, by the coefficient of variation of the Year 1 and Year 2 control plot means of a number of productivity variables (analyzed by-system and by-species).

CHAPTER THREE
GROWTH AND PRODUCTIVITY

Introduction

This chapter is divided into three results sections, that cover the three approaches taken to analysis of the productivity data, and a discussion of these results as a whole. The three approaches to the data analysis are (1) comparison of whole-system productivity of the ten experimental system (monocultures, intercrops, and successional vegetation), (2) comparison of the productivity of each intercrop system with a weighted mean of its component crops grown as monocultures, and (3) comparison of each species' productivity in various crop systems. The first approach compares systems on an absolute basis, without regard for species composition; the second evaluates system response to changes in diversity (spatial mixing of species); the third evaluates individual species' responses to changes in diversity.

The terms "growth" and "productivity" are used in the general sense of biomass accretion per unit time and biomass distribution, rather than as net primary productivity (NPP), which includes drains to herbivores, death, and decomposition (see Methods chapter). The variables used to evaluate productivity of systems and species were divided into those that relate directly to survival and biomass accretion (called "direct" measures) and those that contribute information on the distribution of biomass ("indirect" measures). The direct variables include edible and total aboveground biomass (called "edible biomass"

and "total biomass"); aboveground biomass at flowering (called "biomass at flowering"); root biomass (by two different methods in the two study years); LAI (by the plumb-bob method in both years and also by harvest at flowering in Year 2); a measure of leaf biomass (determined at the time the systems were experimentally defoliated); canopy cover; stem length (agronomic species only); mortality (for each agronomic species); and fullstandedness (percent of full stand count, for each agronomic system as a whole). The indirect measures include allocation ratio (the ratio of edible to total aboveground biomass); root/shoot ratio (at flowering); specific leaf mass (mass per unit leaf area); and a number of "miscellaneous yield measures" that were measured for the four agronomic species, such as maize cob production.

For clarity, most measures of productivity are first examined in control plots to establish baseline trends. Data from the four stress treatments (fertilization, pesticide spraying, defoliation, and watering) are then added to evaluate effects of higher or lower levels of stress compared with the controls, which represent local farmers' conditions. In Year 1, two separate experiments were performed, and the data from them are not mixed. Discussion of Year 1 control plots refers to the large main control plots, while discussion of effects of defoliation refers to the small defoliated plots (and their own controls).

Whenever interaction between cropping system and treatment effects was low ($p_{interaction} > .05$) tests for differences among systems and among treatments were performed on complete samples of all treatments or systems combined to increase the power of the test. When interaction was high ($p_{interaction} < .05$), Duncan's tests for differences among systems and among treatments were performed separately for each treatment and system.

For the sake of expediency in the field, not all measures were taken in all systems and treatments. Such missing blocks of data are omitted from tables and figures or may appear as blanks in tables.

Results: Productivity Differences Among Systems

Measures of Biomass Accretion

Edible and total aboveground biomass at harvest

Control treatment. The mean total biomass of the systems studied ranged from 10-350 g/m^2, and the mean edible biomass ranged from 0-122 g/m^2 (Figures 5 and 6). Edible and total yields were generally the same or slightly lower in Year 2 than Year 1. Edible and total biomass of crop systems containing either maize or sorghum was consistently higher than that of either cowpea or pumpkin monocultures. The difference was significant in all cases except one; pumpkin edible yield was not significantly lower than that of the maize and sorghum monocultures in Year 2, although it was less than half the maize and sorghum edible yields. Total biomass of the successional system was approximately equal to that of the maize- and sorghum-containing crop systems and was also significantly higher than cowpea and pumpkin monocultures. Edible yield of the succession system was assumed to be zero.

Among the crop systems containing monocots, there were no significant differences in total biomass, but there were significant differences in edible biomass in Year 1. Edible yield was significantly lower in the recommended-density maize monoculture than in the sorghum, maize-sorghum, sparse maize, and maize-cowpea systems. The four-crop system had

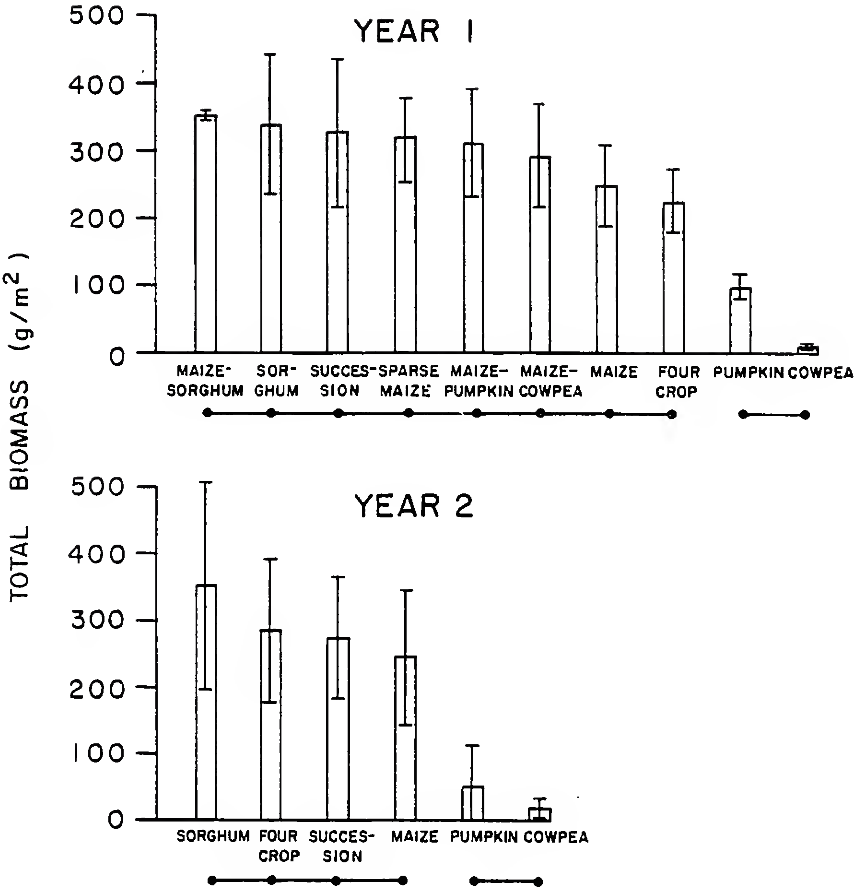

Figure 5. Total aboveground biomass in the control treatment, Years 1 and 2. Systems not sharing a common line are significantly different by Duncan's tests.

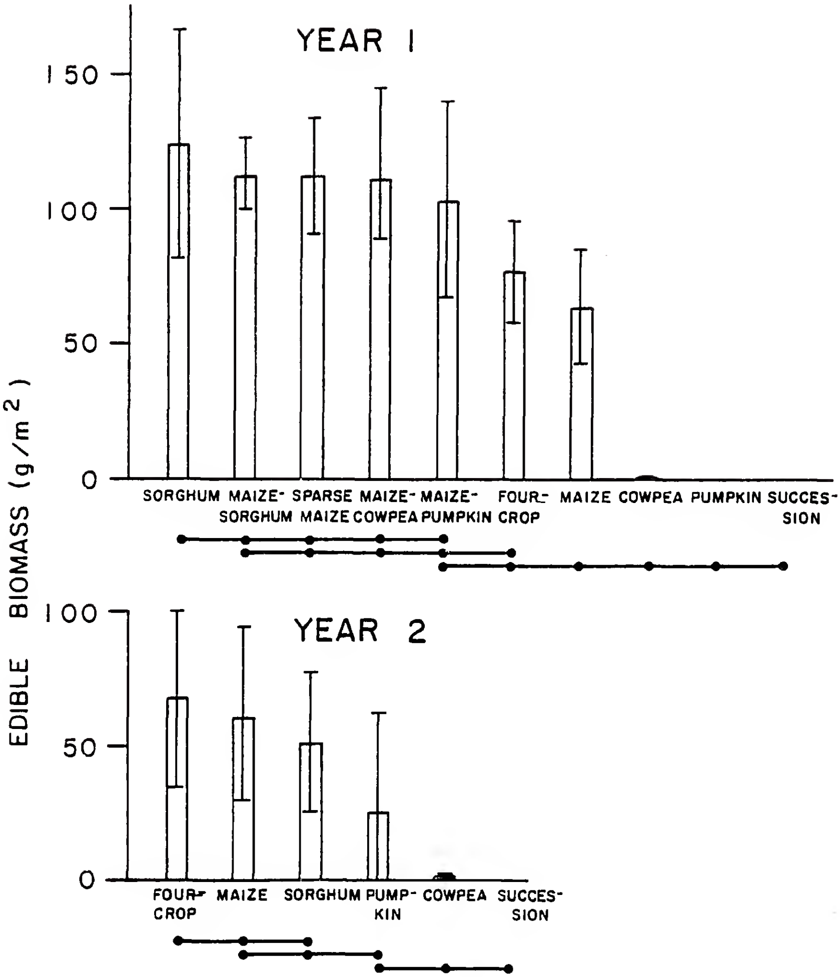

Figure 6. Edible biomass in the control treatment, Years 1 and 2. Systems not sharing a common line are significantly different by Duncan's tests.

the second-lowest edible yield, significantly lower than that of the sorghum monoculture.

Stress Treatments. Defoliation had no consistent or significant effect on whole-system edible and total yield compared with controls (Figures 7-10), except significantly higher total biomass in control than defoliated maize-pumpkin plots in Year 1. When the defoliated leaf biomass was added to the final biomass, this difference was still significant. After adding the defoliated biomass, total production was significantly higher in defoliated than control plots in the maize-cowpea (Year 1) and succession (Years 1 and 2) systems. Thus, all systems except maize-pumpkin recovered from defoliation in terms of edible and total biomass. Significant stimulation of production (when defoliated leaf mass is included in the calculation) was demonstrated in the maize-cowpea and succession systems.

Fertilization significantly increased total aboveground biomass production compared with controls in all systems except cowpea monoculture, and significantly increased edible biomass in all systems except sorghum and cowpea. Edible biomass was, however, more than 50 percent greater in fertilized than control sorghum plots. Watering had no consistent or significant effect on edible and total yield. Pesticide spraying had no effect on total biomass in the maize and sorghum monoculture, but did cause a slight (nonsignificant) increase in the succession system, a large (nonsignificant) increase in cowpea monoculture, and a decrease in the four-crop and pumpkin systems. Spraying decreased edible yield (nonsignificantly) in the maize, pumpkin, and four-crop systems, and substantially (but nonsignificantly) increased it in the sorghum and cowpea monocultures.

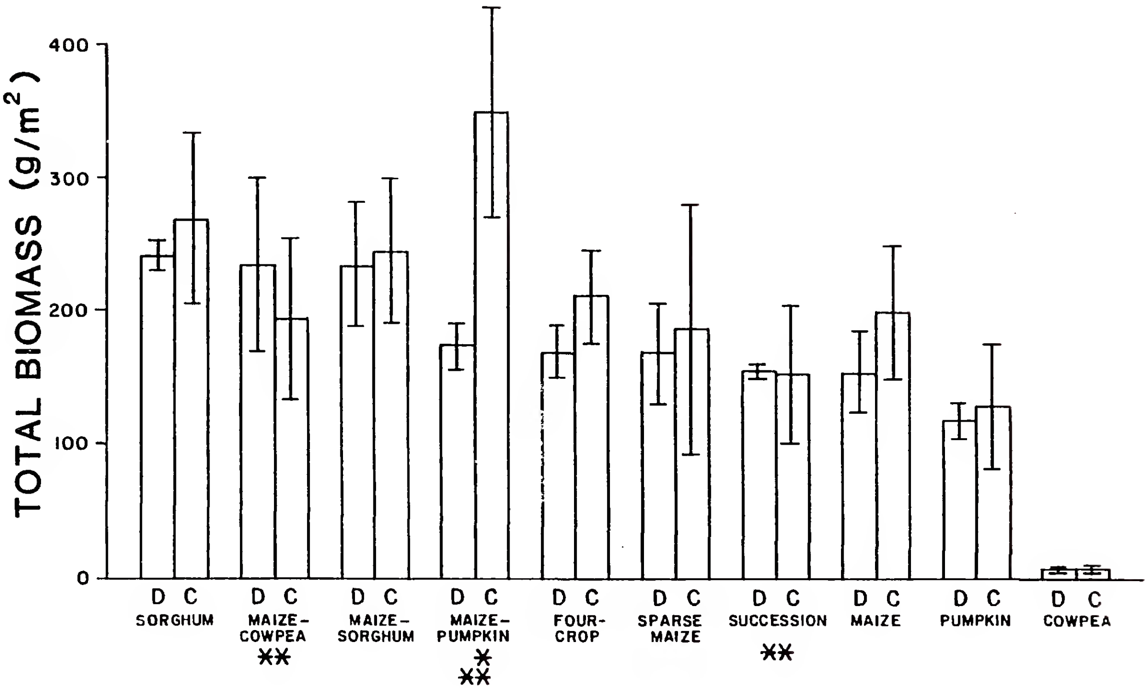

Figure 7. Total aboveground biomass in the control and defoliated treatments, Year 1. All data are from the small Year 1 plots, and mass of defoliated leaves is not included in total biomass. Single asterisk indicates significant difference between control and defoliated treatments by Duncan's tests. Double asterisk indicates significant difference between treatments when defoliated biomass is included in total biomass (defoliated > control in the maize-cowpea and succession systems; control > defoliated in the maize-pumpkin system).

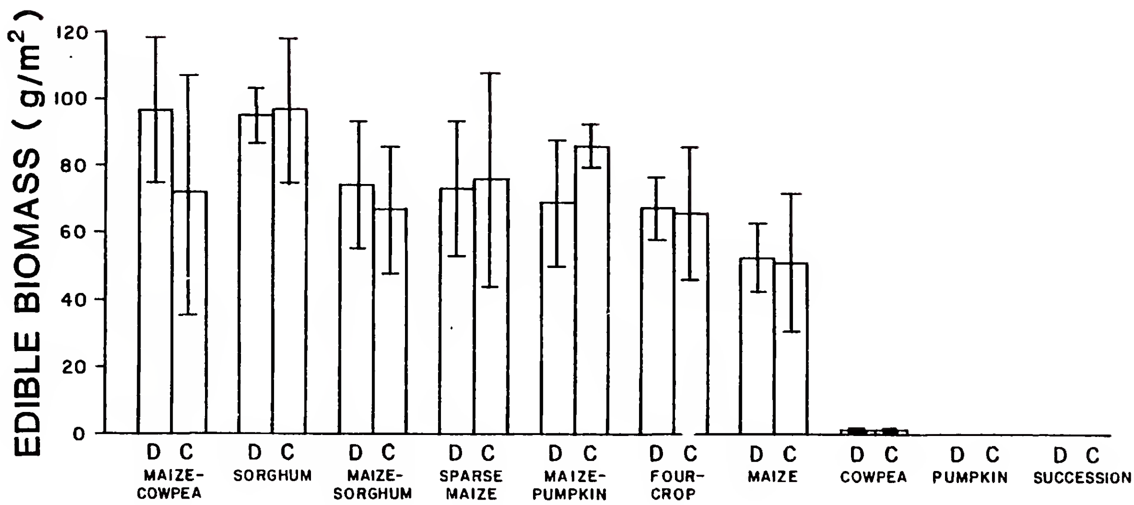

Figure 8. Edible yield in the control and defoliated treatments, Year 1. All data are from the small Year 1 plots. D = defoliation treatment; C = control treatment. Edible yield of control and defoliated plots were not significantly different in any system, by Duncan's tests.

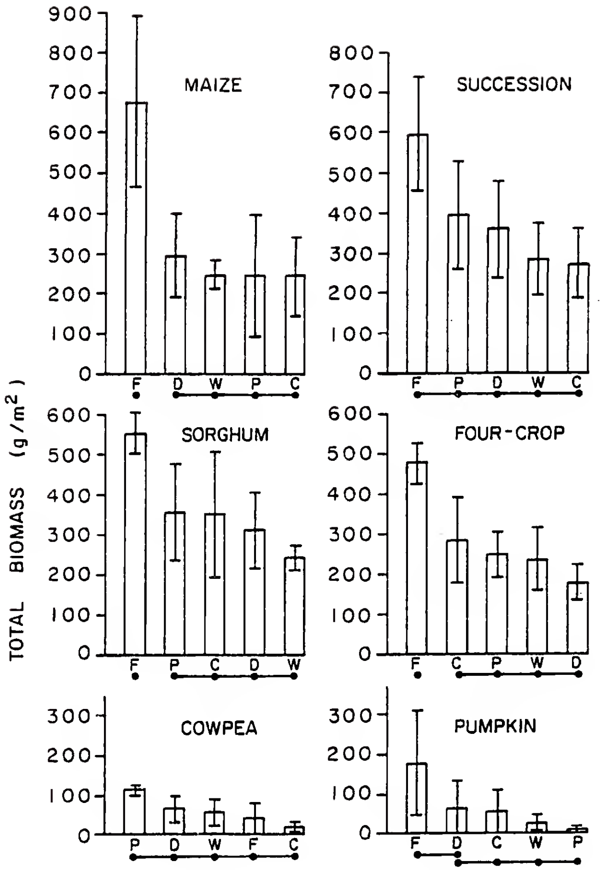

Figure 9. Total aboveground biomass in five treatments, Year 2. C = control treatment, F = fertilized, P = pesticide, D = defoliated, W = watered. Mass of defoliated leaves is not included in total biomass. Treatments not sharing a common line are significantly different by Duncan's tests.

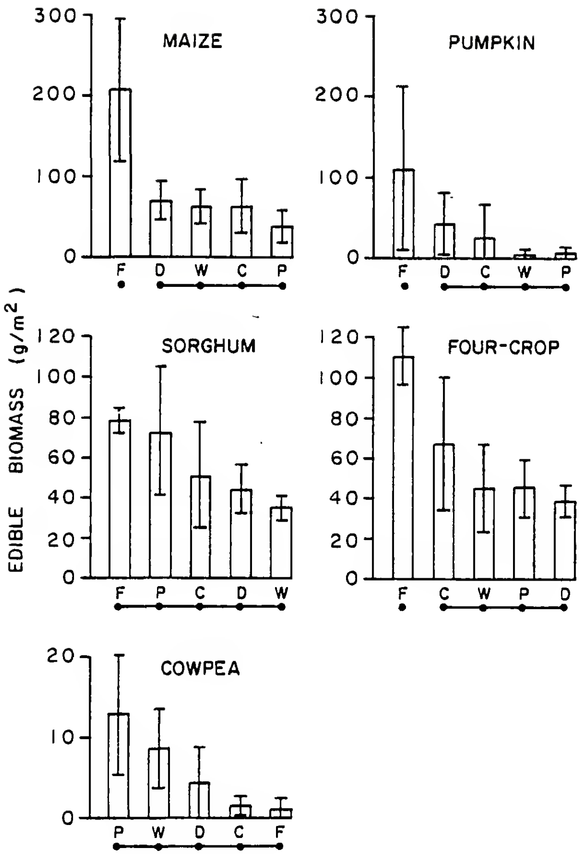

Figure 10. Edible biomass in five treatments, Year 2. C = control treatment, F = fertilized, P = pesticide, D = defoliated, W = watered. Treatments not sharing a common line are significantly different by Duncan's tests.

The ordering of whole-system edible and total biomass varied somewhat among the five stress treatments (Figures 11 and 12). Maize monoculture responded most to fertilization while sorghum monoculture responded little; as a result, maize had the greatest edible and total biomass production in the fertilization treatment. Maize total biomass was significantly higher than all other systems in the fertilization treatment. Pumpkin total biomass increased with fertilization to a level significantly higher than that of cowpea monoculture; pumpkin edible biomass increased to a level not significantly different from that of the four-crop and sorghum systems. Pesticide spraying raised the total biomass of the succession system to first place (significantly higher than that of the four-crop and maize systems), and raised sorghum and cowpea edible biomass relative to the other crop systems. The ordering of systems by total biomass was the same in the watering treatment as in controls, but there were minor changes in the ordering of systems by edible biomass due to slight increases in maize and cowpea edible biomass and slight decreases in the four-crop and pumpkin systems. The defoliated maize-cowpea system was nearly as productive as the highest-yielding system, sorghum monoculture. The four-crop system was adversely affected by defoliation, and as a result its total biomass in the defoliated treatment was significantly lower than that of defoliated succession and not significantly different from that of the two lowest-yielding systems. Edible biomass of the four-crop system was also reduced by defoliation to a level not significantly higher than that of the cowpea and pumpkin monocultures.

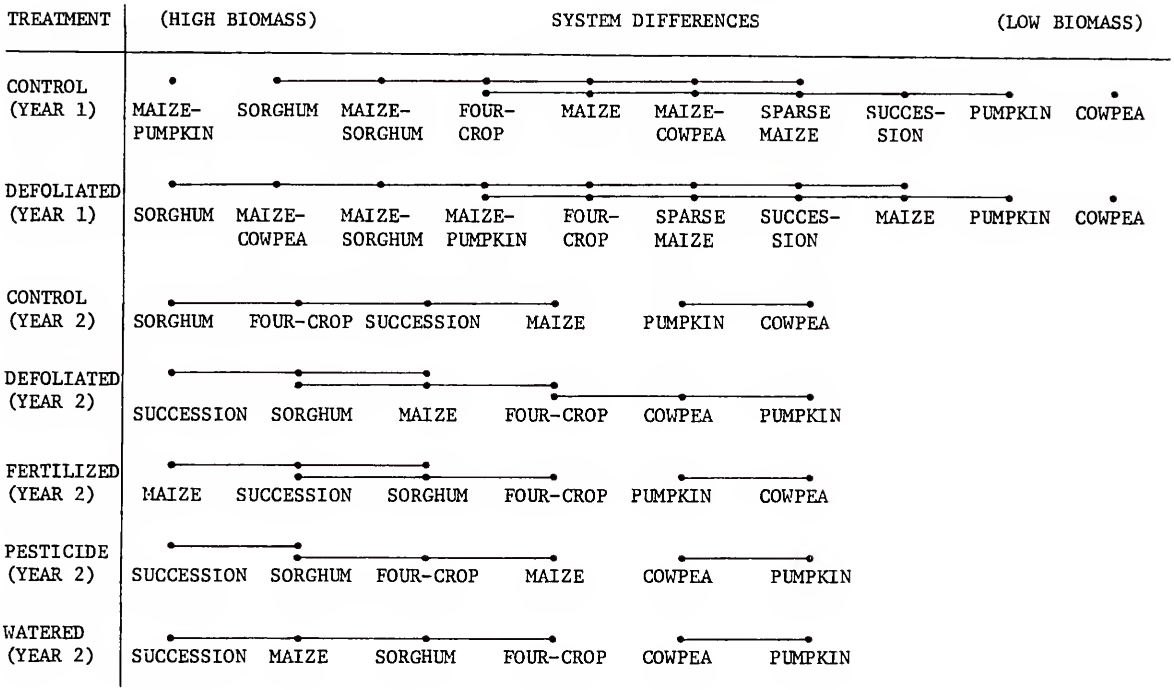

Figure 11. Total aboveground biomass differences among systems, Year 1 and 2. Data are analyzed by-treatment. Year 1 data are from the small control and defoliated plots; Year 2 data are from the indicated treatments. Systems not sharing a common line are significantly different by Duncan's tests. Means and standard deviations are given in Figures 7 and 9.

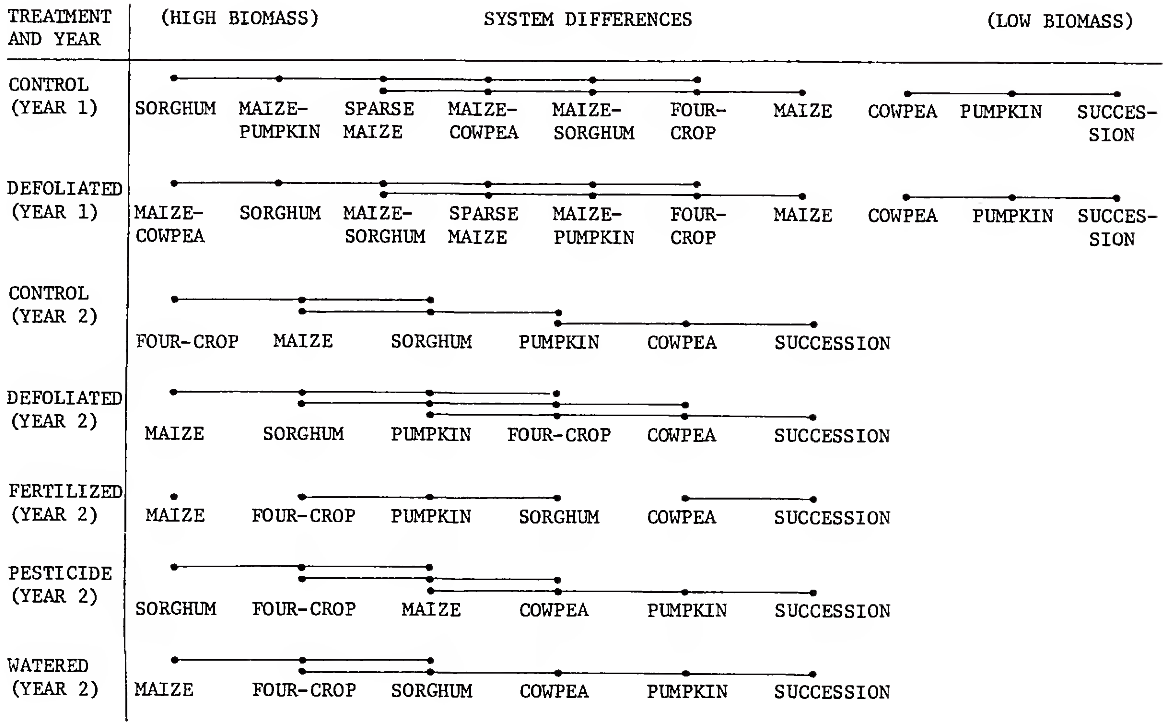

Figure 12. Edible biomass differences among systems, Years 1 and 2. Data are analyzed by-treatment; Year 1 data are from the small control and defoliated plots. Systems not sharing a common line are significantly different by Duncan's tests. Means and standard deviations are given in Figures 8 and 10.

Total aboveground biomass at flowering

Aboveground biomass at flowering (Figure 13) corresponded closely with the final harvest biomass values (r = .91 for all systems and treatments sampled). Biomass at flowering was 50-80 percent of final biomass in the control and fertilized maize, sorghum, four-crop and succession systems. In pumpkin monoculture, biomass did not increase between flowering and the final harvest in control plots, but it did increase dramatically in the fertilization treatment, where biomass at flowering was only 36 percent of final biomass. In cowpea monoculture, biomass increased from flowering to final harvest in control plots, where biomass at flowering was 42 percent of final biomass, but declined by almost 50 percent in the fertilized plots.

In both the control and fertilization treatments, highest biomass at flowering was found in the sorghum monoculture, successional vegetation, and maize monoculture, followed by the four-crop system (Figure 13). Lowest biomass was found in the pumpkin and cowpea monocultures. Biomass at flowering was significantly greater in fertilized than control plots in the sorghum, maize, four-crop, and succession systems.

LAI and canopy cover

Temporal patterns of leaf area development varied from system to system (Figures 14 and 15). Early development of LAI was most rapid in successional vegetation, maize monoculture, maize-sorghum intercrop, and pumpkin monoculture. In the second half of the growing season (after day 46 and day 40 in Years 1 and 2, respectively) successional LAI increased only slightly or declined, whereas LAI of systems containing maize continued

CONTROL		FERTILIZED	
SYSTEM	ABOVEGROUND BIOMASS	SYSTEM	ABOVEGROUND BIOMASS
SORGHUM*	255.20 ± 156.10	MAIZE	490.30 ± 151.15
SUCCESSION*	190.57 ± 72.02	SUCCESSION	475.10 ± 117.27
MAIZE*	181.62 ± 44.93	SORGHUM	467.35 ± 84.24
FOUR-CROP*	144.47 ± 68.28	FOUR-CROP	295.0 ± 17.08
PUMPKIN	53.68 ± 80.27	COWPEA	76.98 ± 78.71
COWPEA	8.28 ± 6.44	PUMPKIN	65.0 ± 57.74

Figure 13. Total aboveground biomass at flowering, Year 2. Entries are $\bar{x} \pm s$, in g/m^2. Systems not sharing a common vertical line are significantly different by Duncan's tests. Asterisks mark systems in which biomass was significantly greater in fertilized than control plots.

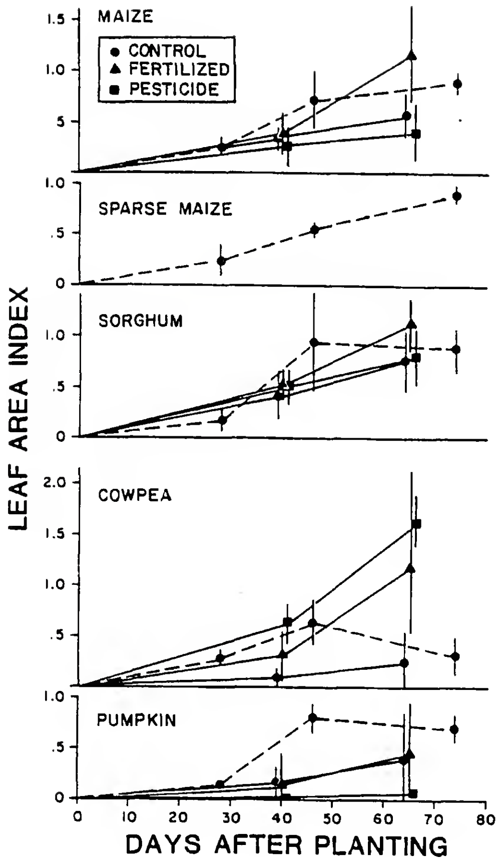

Figure 14. Temporal development of LAI in three treatments in the monoculture systems, Years 1 and 2. Dashed lines are Year 1; solid lines are Year 2.

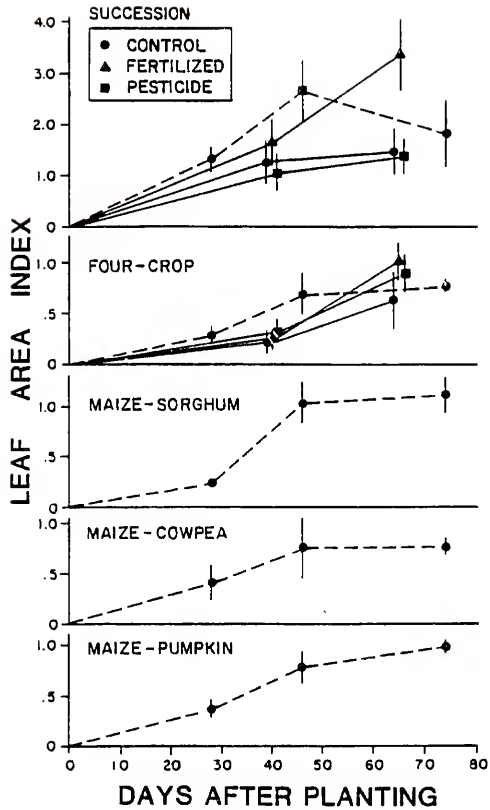

Figure 15. Temporal development of LAI in three treatments in the succession and intercrop systems, Years 1 and 2. Dashed lines are Year 1; solid lines are Year 2. Successional system data were set back seven days by linear interpolation to correct for growth during planting of the crop systems.

to increase. Leaf Area Index in sorghum, cowpea, and pumpkin monocultures declined slightly after day 45 in Year 1. The four-crop system LAI stayed the same or increased slightly during the second half of the growing season.

The LAI in fertilized and pesticide-sprayed plots was not significantly different from controls in the first LAI sample in any system, but LAI was higher in fertilized plots than in the other treatments in most systems (Figure 16). In the second LAI sample, LAI was significantly higher in fertilized plots than in both control and pesticide plots in maize monoculture and succession, and nonsignificantly higher in the sorghum, pumpkin, and four-crop systems. Both fertilization and pesticide spraying significantly increased the LAI of cowpea monoculture compared with controls. Effects of fertilization were especially evident in all systems at the end of the growing season.

Successional LAI was significantly greater than that of all other systems in control plots in both study years (Figure 17). The cowpea and pumpkin monocultures consistently had the lowest LAI in control plots. The ordering of systems by LAI was changed somewhat in the stress treatment. Cowpea LAI was the highest of all systems including succession in the pesticide treatment, significantly higher than that of the maize, sorghum, and pumpkin monocultures. The LAI of the four-crop system responded positively, and that of maize and pumpkin monocultures negatively, to pesticide spraying.

Canopy cover followed much the same patterns of development as LAI (Figures 18 and 19). Canopy cover was consistently higher in Year 1 than Year 2. Successional ground cover increased rapidly during the

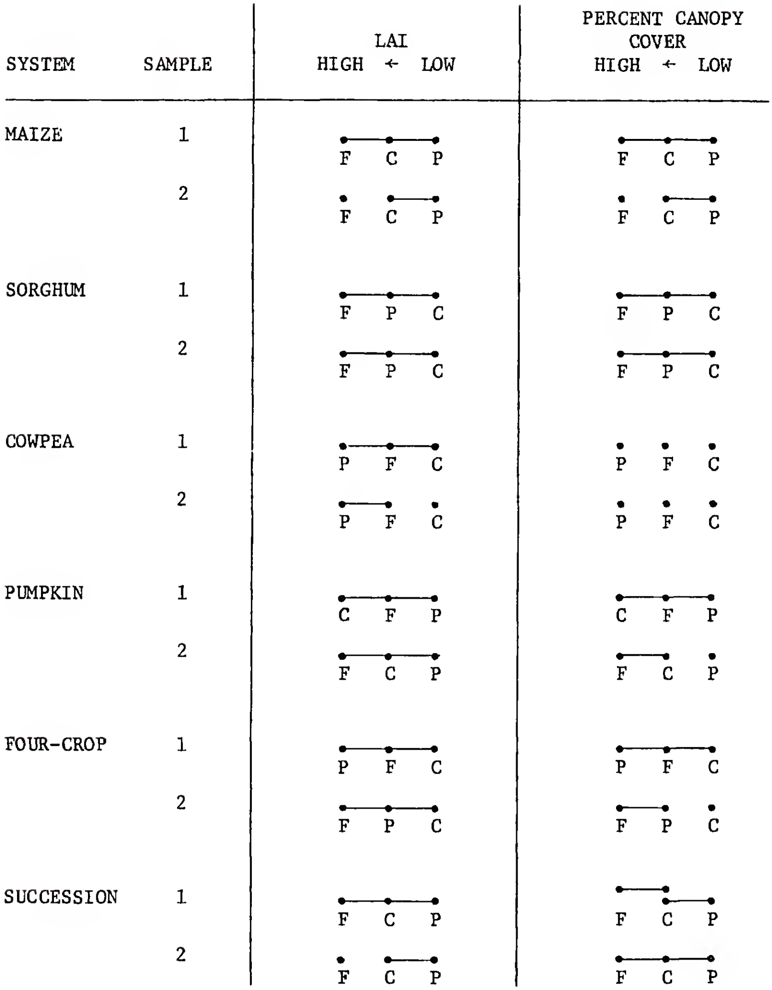

Figure 16. System LAI and canopy cover differences among treatments, Year 2. C=control treatment; F=fertilized; P=pesticide. Treatments not sharing a common line are significantly different by Duncan's tests.

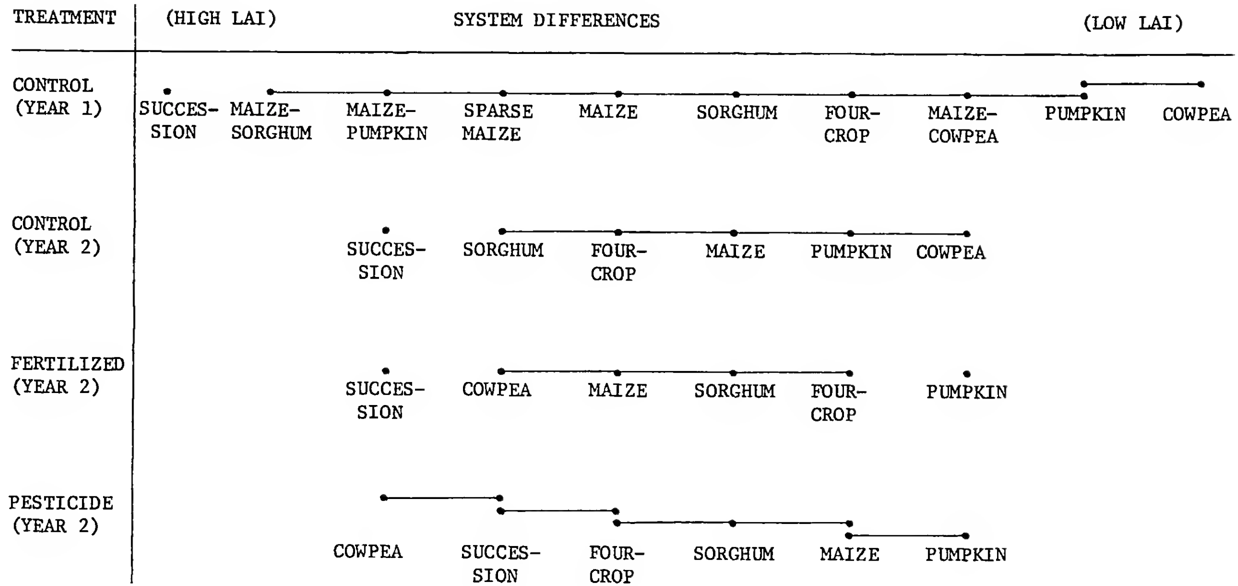

Figure 17. LAI differences among systems, Years 1 and 2. Data are from sample 3 in Year 1 and sample 2 in Year 2 (the samples most representative of overall LAI development). Year 1 data are from the main control plots; Year 2 data are from the indicated treatments. Systems not connected by a common line are significantly different by Duncan's tests.

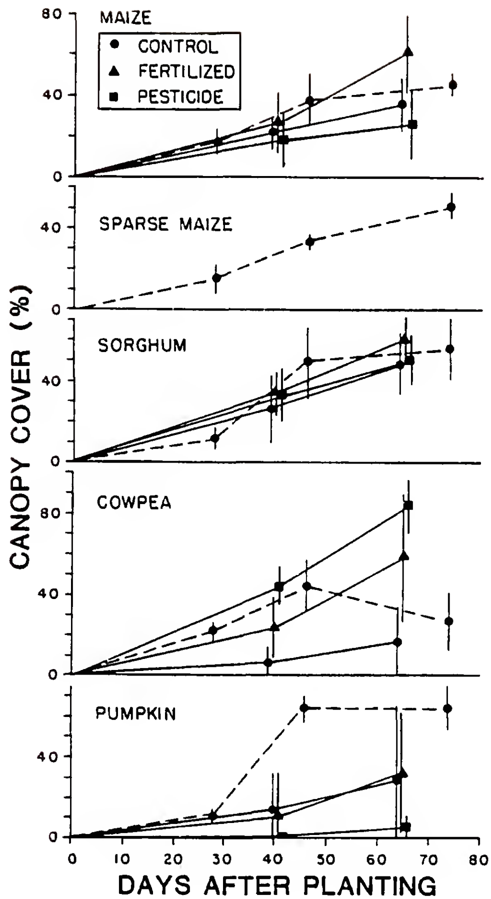

Figure 18. Temporal development of canopy cover in three treatments in the monoculture systems, Years 1 and 2. Dashed lines are Year 1; solid lines are Year 2.

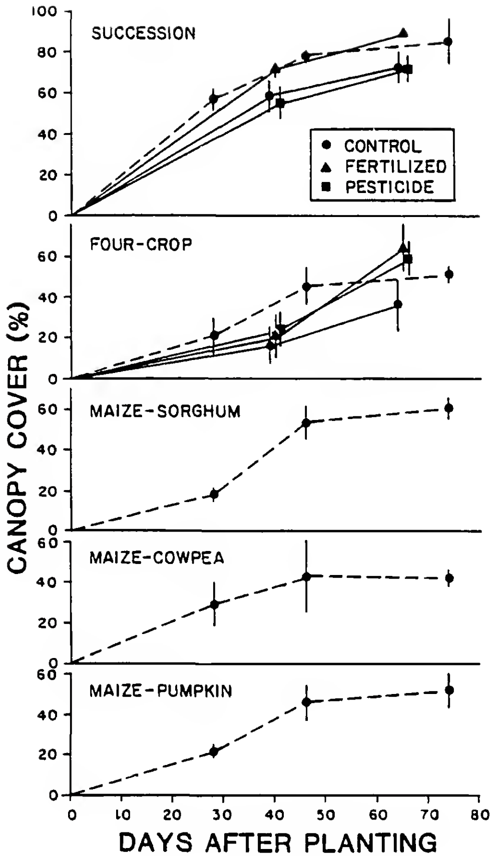

Figure 19. Temporal development of canopy cover in three treatments in the succession and intercrop systems, Years 1 and 2. Dashed lines are Year 1; solid lines are Year 2. Succession system data were set back seven days by linear interpolation to correct for growth during planting of the crop systems.

first sampling period in both years and continued to maxima in control plots of approximately 85 and 70 percent in Years 1 and 2, respectively. In both Year 1 samples, successional canopy cover was significantly higher than that of all other systems (except pumpkin monoculture in sample 2); in Year 2 it was significantly higher than any other system in the control and fertilized treatments.

Pumpkin monoculture developed more complete canopy cover in Year 1 than expected from its low LAI; its 65 percent cover was the highest of all agricultural systems, significantly higher than that of several other cropping systems. In Year 2, pumpkin canopy cover was also relatively high compared to its LAI, but was nevertheless the lowest of all systems under all three stress treatments. Canopy cover was lowest in the maize-cowpea system in Year 1, and in cowpea and pumpkin monocultures in Year 2 control and fertilized plots. Cowpea canopy cover was the highest of all systems in the pesticide treatment, however. The ordering of systems by canopy cover in the fertilization and pesticide treatments was the same as the ordering by LAI (Figures 17 and 20); the fertilization and pesticide treatments also had the same effects on each system's canopy cover as on LAI, although there were some minor differences in the degree of significance (Figure 16).

LAI at flowering

System LAI at flowering in Year 2 (harvest method) was significantly lower in the cowpea monoculture than in the maize and four-crop systems, and was significantly higher in fertilized than control plots (Figure 21). The LAI at flowering by the harvest method tended to be slightly higher

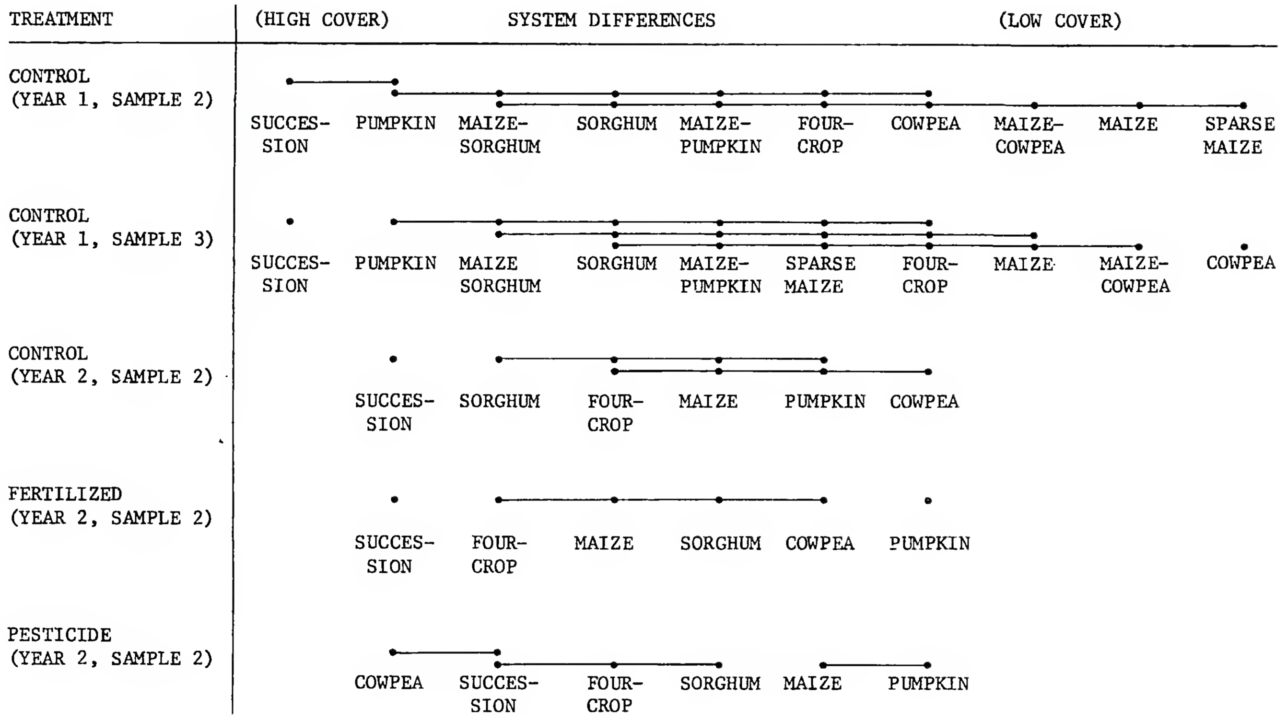

Figure 20. Canopy cover differences among systems, Years 1 and 2. Year 1 data are from the main control plots; Year 2 data are from the indicated treatments. Systems not sharing a common line are significantly different by Duncan's tests.

CONTROL		FERTILIZED	
SYSTEM	LAI	SYSTEM	LAI
MAIZE	.74 ± .17	MAIZE	1.56 ± .43
PUMPKIN	.71 ± 1.00	FOUR-CROP	1.12 ± .15
FOUR-CROP	.59 ± .23	SORGHUM	1.06 ± .20
SORGHUM	.54 ± .29	PUMPKIN	.80 ± .50
COWPEA	.09 ± .06	COWPEA	.74 ± .74

Figure 21. LAI at flowering, Year 2. Entries are $\bar{x} \pm s$. Systems not sharing a common vertical line are significantly different by Duncan's tests, performed on a complete sample of both treatments combined. LAI of fertilized plots was significantly greater than that of controls by Duncan's test, performed on a sample of all systems combined.

than LAI determined by the plumb-bob method (Table 5). Higher values are expected by the harvest method because it measures actual leaf surface area, rather than leaf surface area as it would project onto a horizontal surface. Sorghum LAI tended to be higher by the plumb-bob method, possibly because of early cessation of leaf production (hence an overestimate by extrapolation of early plumb-bob values). Cowpea LAI was also slightly higher by the plumb-bob method in control plots. This may have been due to applying day 71 specific leaf mass values to the day 51 cowpea harvest. Cowpea specific leaf mass increased from day 40-71, from 44.5 to 63.6 g/m^2 in control plots, and from 31.6 to 54.9 g/m^2 in fertilized plots.

Leaf mass at defoliation

Half the leaf area was removed with accuracy during the defoliation treatment, and the mass of defoliated leaves was used as a measure of leaf production. More than half of the leaves were removed from the successional vegetation, however (approximately 71 and 57 percent of LAI in Years 1 and 2, respectively). The mass of defoliated leaves was significantly greater in succession than in all other systems in both study years; it is likely that the differences would also have been significant if exactly half the leaf area had been removed and a correction made for the slightly greater age of the successional vegetation than that of the crop systems. Among the crop systems, defoliated leaf mass was greatest in the maize-cowpea system in Year 1; maize and cowpea monocultures also had relatively high defoliated leaf biomass in both years. Leaf mass at defoliation was relatively low in the sorghum, four-crop, and pumpkin systems (Figure 22).

Table 5. Comparison of LAI by the plumb-bob and harvest methods in monocultures, Year 2. Plumb-bob values are interpolated or extrapolated to the harvest sample date (approximate date of flowering: day 52 for cowpeas; day 73, sorghum; day 77, maize; day 79, pumpkin).

	CONTROL		FERTILIZED	
SYSTEM	PLUMB-BOB	HARVEST	PLUMB-BOB	HARVEST
MAIZE MONOCULTURE	.66	.74	1.51	1.56
SORGHUM MONOCULTURE	.88	.54	1.31	1.06
COWPEA MONOCULTURE	.17	.09	.72	.81
PUMPKIN MONOCULTURE	.53	.71	.62	.80

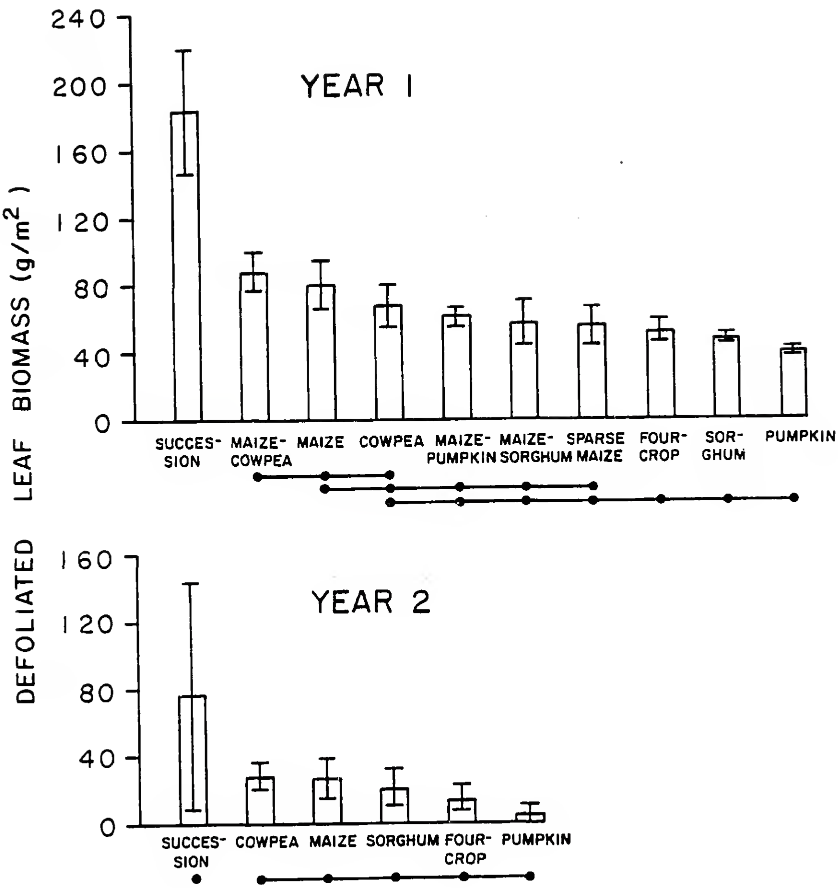

Figure 22. Leaf mass at defoliation, Years 1 and 2. Systems not sharing a common line are significantly different by Duncan's tests.

Root biomass

Root biomass to 40 cm in Year 1 was greatest in the four-crop and successional systems; the four-crop system had significantly higher root biomass than any other agronomic system (Figure 23). Root biomass was lowest in the pumpkin, sorghum, and maize-cowpea systems, but the differences were not significant. Experimental error by this method was high due to the patchiness of agronomic root systems (high point-to-point variability), small core diameter, and low sample size (five to ten cores per system).

Year 2 root biomass to 15 cm by the harvest method was significantly greater in successional vegetation and sorghum monoculture (27.6 and 24.0 g/m^2, respectively) than the other four agronomic systems (ranging from 1.2-10.9 g/m^2) in control plots (Figure 24). In fertilized plots, sorghum rooting (mean 47.6 g/m^2) was significantly greater than that of any other system, followed by the maize, four-crop, and succession systems. Fertilized cowpea and pumpkin monocultures had significantly lower root biomass than all other fertilized systems. Roots were significantly more abundant in fertilized than control plots in the sorghum, maize, and four-crop systems; the pumpkin monoculture and successional vegetation had about the same root biomass in control and fertilized plots. Coefficient of variation of root biomass in the 6 and 12 m^2 harvested plots (Year 2) were lower than those from the smaller soil cores (Year 2).

Surface root biomass in the two study years was roughly comparable despite the differences in methods used. Year 1 mean root biomass (by

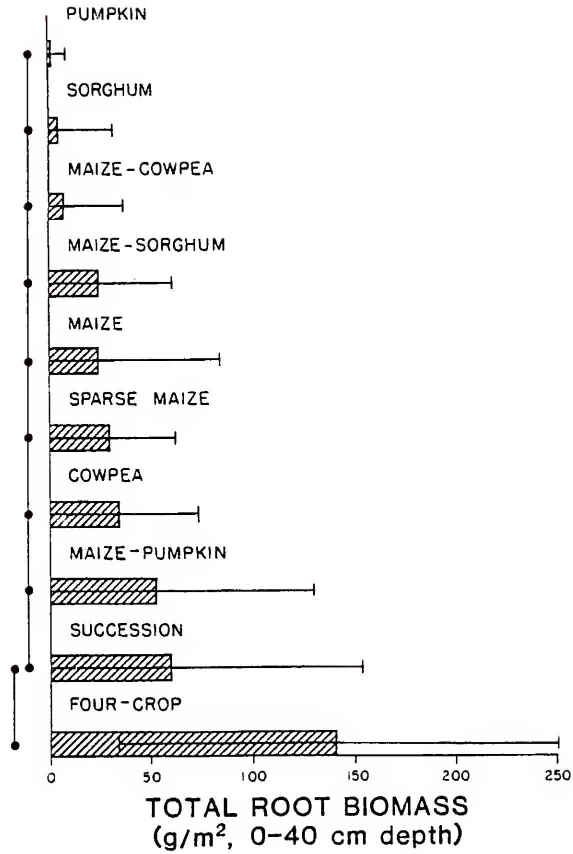

Figure 23. Root biomass, 0-40 cm, Year 1. Root biomass in bare ground plots was subtracted from all other systems to correct for residual roots from previous vegetation. Systems not connected by a common vertical line are significantly different by Duncan's test.

CONTROL		FERTILIZED	
SYSTEM	ROOT BIOMASS	SYSTEM	ROOT BIOMASS
SUCCESSION	27.57 ± 15.27	SORGHUM	47.60 ± 11.43
SORGHUM*	23.94 ± 15.80	MAIZE	34.53 ± 10.49
FOUR-CROP*	10.88 ± 4.34	FOUR-CROP	28.87 ± 3.47
MAIZE*	9.83 ± 1.19	SUCCESSION	20.16 ± 7.20
COWPEA	2.05 ± .70	COWPEA	7.65 ± 3.74
PUMPKIN	1.25 ± 1.64	PUMPKIN	1.63 ± 1.46

Figure 24. Root biomass at flowering, 0-15 cm, Year 2. Entries are $\bar{x} \pm s$, in g/m^2. Systems not sharing a common vertical line are significantly different by Duncan's tests. Asterisks mark systems in which root biomass was significantly greater in fertilized than control plots by Duncan's tests, performed on samples of both treatments combined.

system, 0-10 cm) ranged from 0-36 g/m^2; Year 2 means (by system, control plots only, 0-15 cm) ranged from 1-28 g/m^2.

System fullstandedness

Establishment and maintenance of the desired planting stand density is indicated by the variable called fullstandedness (sum of percent full stand of a system's component crops, Figures 25 and 26). Establishment was good in Year 1, and fullstandedness on the first sampling date was approximately 100 (the desired planting density) in all systems. In Year 2 pumpkin germination was poor, depressing fullstandedness of both the four-crop and pumpkin monoculture systems, but the other systems achieved approximately the desired planting densities. Early cowpea mortality and later pumpkin mortality reduced the fullness of the cowpea, maize-cowpea, pumpkin, and four-crop systems in Year 1. In Year 2, cowpea and pumpkin mortality again reduced the fullness of the cowpea, four-crop, and pumpkin stands (although cowpea mortality was lower in the pesticide, fertilization, and watering treatments). In both years, the fullest end-of-season stands occurred in monocultures of species with low mortality rates, the least full stands were in monocultures of species with high mortality rates, and the intercrop systems composed of both high and low mortality species were intermediate in fullstandedness. The maize-sorghum intercrop, composed of two low mortality crops, had the highest fullstandedness of any system in Year 1.

No significant effects of treatments on fullstandedness were found in the first sample, but in sample 2 the watered treatment had significantly fuller stands than the control, fertilization, and

SAMPLE	SYSTEM DIFFERENCES								
1	MAIZE-SORGHUM 103.7	FOUR-CROP 100.8	SORGHUM 100.6	MAIZE-PUMPKIN 98.8	PUMPKIN 97.1	MAIZE-COWPEA 97.0	COWPEA 95.6	MAIZE 94.2	SPARSE MAIZE 44.5
2	MAIZE-SORGHUM 99.2	PUMPKIN 97.1	FOUR-CROP 95.0	MAIZE-PUMPKIN 93.9	SORGHUM 92.8	MAIZE 91.4	MAIZE COWPEA 84.8	COWPEA 70.4	SPARSE MAIZE 43.6
3	MAIZE-SORGHUM 93.6	MAIZE 91.9	MAIZE-PUMPKIN 91.4	SORGHUM 87.7	FOUR-CROP 79.0	PUMPKIN 78.2	MAIZE-COWPEA 71.2	COWPEA 48.4	SPARSE MAIZE 44.3

Figure 25. System fullstandedness differences among systems, Year 1. Data are from main control plots and three sampling times.

SAMPLE	TREATMENT	SYSTEM DIFFERENCES				
1	ALL	MAIZE 105.7	COWPEA 95.9	SORGHUM 92.2	FOUR-CROP 76.4	PUMPKIN 29.5
2	ALL	MAIZE 103.8	SORGHUM 87.8	COWPEA 87.3	FOUR-CROP 71.5	PUMPKIN 31.1
3	CONTROL	MAIZE 90.6	SORGHUM 79.8	COWPEA 70.2	FOUR-CROP 68.6	PUMPKIN 35.3
	FERTILIZED	MAIZE 89.6	SORGHUM 81.3	COWPEA 78.3	FOUR-CROP 66.9	PUMPKIN 23.6
	PESTICIDE	COWPEA 91.3	SORGHUM 85.1	MAIZE 81.2	FOUR-CROP 63.0	PUMPKIN 10.6
	DEFOLIATED	MAIZE 92.5	COWPEA 80.4	SORGHUM 77.4	FOUR-CROP 55.3	PUMPKIN 18.36
	WATERED	MAIZE 98.7	COWPEA 83.3	SORGHUM 80.4	FOUR-CROP 73.7	PUMPKIN 31.5

Figure 26. System fullstandedness differences among systems, Year 2. Means (percent of target planting density) are given below each system; values > 100 indicate overplanting. Systems not sharing a common line are significantly different by Duncan's tests (performed on samples of all treatments combined in samples 1 and 2, and performed by-treatment in sample 3).

pesticide treatments (Figure 27). In sample 3 the stress treatments had no effect on stand fullness in the maize, sorghum, and four-crop systems, but pesticide-treated cowpea plots were significantly fuller than controls, and sprayed and defoliated pumpkin plots were less full than controls.

Measures of Biomass Distribution

Percent monocot LAI

All three Year 1 mixed monocot-dicot intercrop systems had higher proportions of monocot leaf area than expected from the proportions of monocots planted and significantly higher percent monocot LAI than that of the succession system (48 percent, Figure 28). The four-crop system was the most similar to the succession system in terms of percent monocot LAI, although the monocot component of the four-crop system increased after the second LAI sample to a level not significantly different from that of the maize-pumpkin and maize-cowpea systems. In Year 2, successional vegetation again had a lower percent monocot LAI than the four-crop system in both control and fertilized plots (significantly lower in fertilized plots in sample 2).

Pesticide spraying significantly reduced the percent of monocot leaf area in the four-crop system (compared with control and fertilized plots) and slightly increased percent monocot LAI in the succession system. As a result, percent monocot LAI of the four-crop and succession system did not differ significantly in the pesticide treatment. Fertilization increased percent monocot LAI (compared with pesticide and control plots) in both four-crop and successional systems (Figure 29).

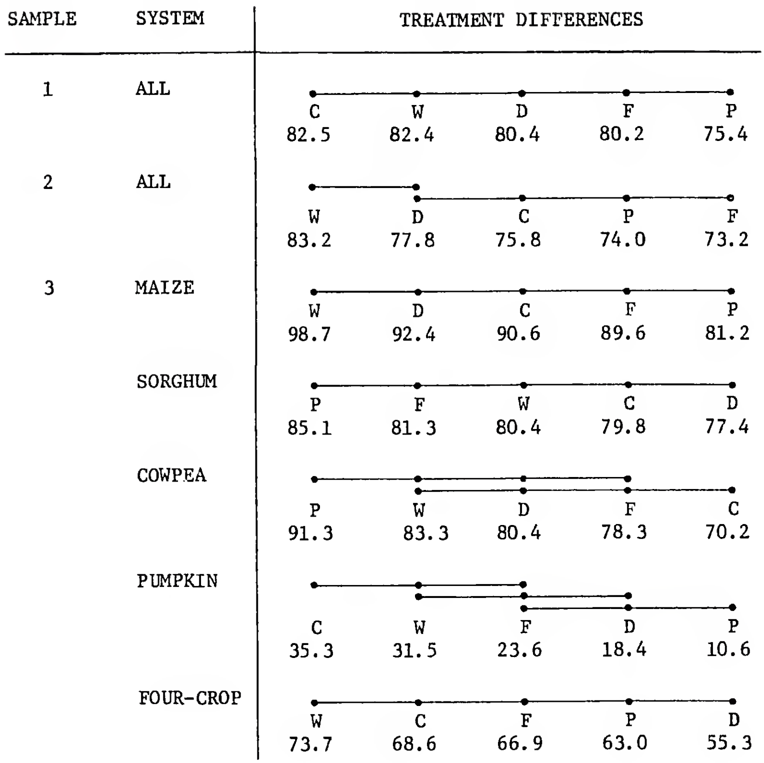

Figure 27. System fullstandedness differences among treatments, Year 2. C=control treatment; P=pesticide; D=defoliated; W=watered. Systems not sharing a common line are significantly different by Duncan's tests (performed on a sample of all systems combined in samples 1 and 2, and performed by-system in sample 3).

TREATMENT	YEAR 1, SAMPLE 2				YEAR 1, SAMPLE 3			
CONTROL	MAIZE-PUMPKIN 83.7	MAIZE-COWPEA 78.6	FOUR-CROP 65.8	SUCCES-SION 47.7	MAIZE-PUMPKIN 86.9	MAIZE-COWPEA 84.6	FOUR-CROP 83.7	SUCCES-SION 47.9

TREATMENT	YEAR 2, SAMPLE 1		YEAR 2, SAMPLE 2	
CONTROL	FOUR-CROP 82.2	SUCCESSION 55.4	FOUR-CROP 63.8	SUCCESSION 42.1
FERTILIZED	FOUR-CROP 76.5	SUCCESSION 65.1	FOUR-CROP 69.8	SUCCESSION 62.3
PESTICIDE	SUCCESSION 59.4	FOUR-CROP 54.4	SUCCESSION 47.8	FOUR-CROP 43.1

Figure 28. Percent monocot LAI differences among systems, Years 1 and 2. Year 1 data are from the main control plots; Year 2 data are from the indicated treatments.

SYSTEM	SAMPLE	TREATMENT DIFFERENCES		
FOUR-CROP	1	C 82.2	F 76.5	P 54.4
	2	F 69.8	C 63.8	P 43.1
SUCCESSION	1	F 65.1	P 59.4	C 55.4
	2	F 62.3	P 43.1	C 42.1

Figure 29. Percent monocot LAI differences among treatments, Year 2. C = control treatment; F = fertilized; P = pesticide. Treatments not sharing a common line are significantly different by Duncan's tests.

Allocation ratios

The ratio of edible to total aboveground biomass (allocation ratio) in Year 1 was highest in the maize-cowpea, sorghum, and sparse maize systems, followed by the four-crop, maize-pumpkin, maize-sorghum, and maize systems; allocation ratio was lowest in the cowpea and pumpkin systems (Figure 30). In Year 2 (Figure 31), pumpkin allocation ratio was the highest of all systems in control plots, but cowpea allocation ratio was again very low. System allocation ratios tended to be lower in Year 2 than Year 1.

In Year 1, defoliation significantly increased allocation ratios in a sample of all systems combined, but in Year 2 the four stress treatments had no significant effect on allocation ratios in a sample of all systems combined. Treatment effects did cause minor changes in the ordering of systems by allocation ratio in Year 2, however (Figure 31); in the pesticide treatment sorghum allocation ratios were higher, and pumpkin allocation ratios lower, than in controls.

Root/shoot ratios

The ratio of root biomass (0-15 cm) to total aboveground biomass, at flowering, was highest in cowpea monoculture and lowest in sorghum, maize, and pumpkin monocultures (Figure 32). The succession and four-crop systems were intermediate; root/shoot ratios were significantly higher in control than in fertilized plots in the cowpea, pumpkin, and succession systems (Figure 33). In the maize, sorghum, and four-crop systems the ratio was slightly (nonsignificantly) higher in fertilized plots than in controls.

MAIZE-COWPEA	SORGHUM	SPARSE MAIZE	FOUR-CROP	MAIZE PUMPKIN	MAIZE-SORGHUM	MAIZE	COWPEA	PUMPKIN
.38	.36	.35	.34	.33	.32	.26	.07	0

Figure 30. System allocation ratio differences among systems, Year 1. Data are from the main control plots. Systems not sharing a common line are significantly different by Duncan's tests.

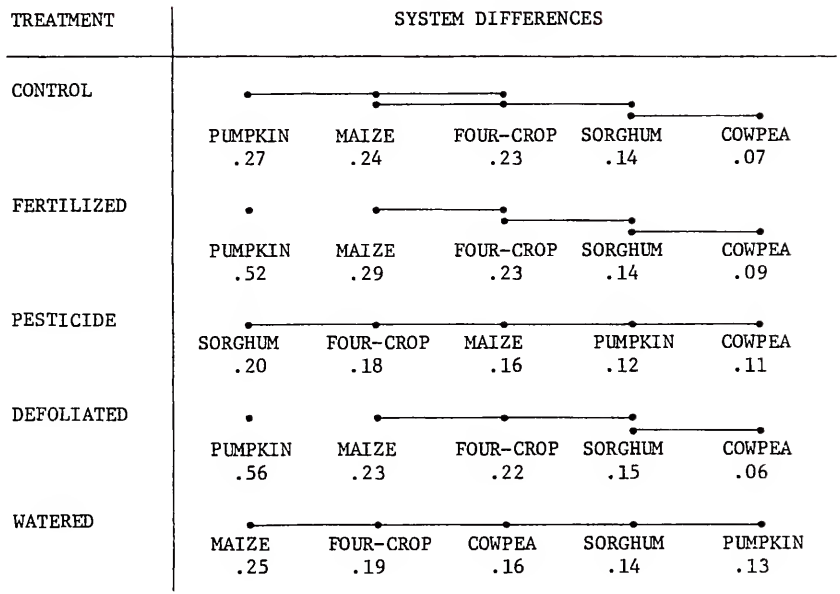

Figure 31. System allocation ratio differences among systems, Year 2. Systems not sharing a common line are significantly different by Duncan's tests.

TREATMENT	SYSTEM DIFFERENCES					
CONTROL	COWPEA	SUCCESSION	SORGHUM	FOUR-CROP	MAIZE	PUMPKIN
	.315	.138	.092	.076	.056	.035
FERTILIZED	COWPEA	SORGHUM	FOUR-CROP	MAIZE	SUCCESSION	PUMPKIN
	.199	.101	.098	.072	.042	.025

Figure 32. Root/shoot ratios at flowering, differences among systems, Year 2. Systems not sharing a common line are significantly different by Duncan's tests.

SYSTEM	TREATMENT DIFFERENCES	
MAIZE	FERTILIZED .072	CONTROL .056
SORGHUM	FERTILIZED .101	CONTROL .092
COWPEA	CONTROL .315	FERTILIZED .199
PUMPKIN	CONTROL .035	FERTILIZED .025
FOUR-CROP	FERTILIZED .098	CONTROL .076
SUCCESSION	CONTROL .138	FERTILIZED .042

Figure 33. Root/shoot ratios at flowering, differences among treatments, Year 2. Treatments not sharing a common line are significantly different by Duncan's tests.

Correlations Among Productivity Variables

Many of the direct measures of biomass accretion were strongly positively intercorrelated (Table 6). The correlation coefficients are based on all plots of all systems and treatments in which each pair of measurements was taken; the greatest source of variation (and correlation) is expected to be effects of species composition rather than treatment effects or experimental error. One variable that was not particularly well-correlated with the productivity measures was edible biomass. It was negatively correlated with leaf mass at defoliation, canopy cover, and LAI, probably due to the edible yield failure of cowpea and pumpkin despite their relatively abundant early vegetative growth.

Some measures of biomass distribution ("indirect" productivity measures) were also strongly correlated with the measures of biomass accumulation ("direct" measures) (Table 6). Abundance of monocots was strongly positively correlated with all productivity variables except LAI (second sample) and canopy cover. Root/shoot ratios were strongly negatively correlated with many aboveground productivity measures, but uncorrelated with fullstandedness and with root biomass. Allocation ratios were strongly positively correlated with both edible and total biomass in Year 1, and with edible (but not total) biomass in Year 2. Allocation ratios were positively correlated with LAI at flowering in Year 2, but negatively correlated with LAI by the plumb-bob method. Root/shoot ratios were highly negatively correlated with allocation ratios.

Table 6. Correlations among direct and indirect system productivity measures, Years 1 and 2. Direct = measures of biomass accretion; indirect = measures of biomass distribution. Experiment 1 = Year 1 main plots; 2 = Year 1 control and defoliated plots; 3 = all Year 2 plots. Values are Pearson product-moment correlation coefficients, based on samples of all plots (of all systems and treatments) in which each pair of measures was taken. Correlations involving edible biomass, fullstandedness, and allocation ratio exclude successional vegetation plots.

	EXPERIMENT	BIOMASS[a]	BIOMASS[b]	EDIBLE BIOMASS[a]	DEFOLIATED BIOMASS[c]	LAI[d]	LAI[b]	CANOPY COVER[d]	FULLSTANDEDNESS[e]	PERCENT MONOCOT LAI[d]	ROOT BIOMASS[b]	ROOT/SHOOT[b]	ALLOCATION RATIO[a]
BIOMASS[b]	3	.91‡											
EDIBLE BIOMASS[a]	1	.72‡											
	2	.82‡											
	3	.58‡	.45‡										
DEFOLIATED BIOMASS[c]	2	.00		-.10									
	3	.51‡		-.28									
LAI[d]	1	.18		-.39†									
	3	.46‡	.48‡	-.17									
LAI[b]	3	.63‡	.70‡	.66‡									
CANOPY COVER[d]	1	.14		-.38									
	3	.54‡	.66‡				.79‡						
FULLSTANDEDNESS	1	.05		-.05			.50‡	.48†					
	3	.43†	.49†	.23†	.72†	.52†	.25	.54†					

Table 6--extended.

PERCENT MONOCOT LAI[d]	1	.74‡		.80‡		−.13		−.39†	.34			
	3	.65‡	.65‡	.42‡	.24	.08	.30†	.15	.56†			
ROOT BIOMASS[b]	3	.75‡	.83‡	.36‡		.37‡	.54‡	.53‡	.41†	.63‡		
ROOT/SHOOT[b]	3	−.32‡	−.29†	−.30†		−.23	−.42†	−.24	.18	−.25†	−.03	
ALLOCATION RATIO[a]	1	.55‡		.93‡		−.44‡		−.49‡	.20	.80‡		
	2	.39‡		.78‡	−.12							
	3	.02	−.08	.58‡	−.43‡	−.28‡	.41‡	−.12	−.26†	−.01	−.16	−.36‡

[a]at final harvest

[b]at flowering

[c]defoliated plots only

[d]second LAI/canopy cover sample

[e]third stand count

†significant at $p < .05$

‡significant at $p < .01$

Year-to-Year Productivity Differences

Year-to-year differences in productivity can be summarized by comparison of five productivity measures taken in both study years (Table 7). LAI and canopy cover were lower in Year 2 than in Year 1 in all systems. Edible biomass, total biomass, and fullstandedness were approximately the same in both years in the maize, sorghum, and four-crop systems. Cowpea LAI and canopy cover were higher in Year 1 than Year 2 in the middle of the growing season, but end-of-season fullstandedness, edible biomass, and total biomass were lower in Year 1. Pumpkin stand count, LAI, canopy cover, and total biomass were higher in Year 1 than Year 2, but edible yield was higher in Year 2. Production in the successional system was lower in Year 2 than Year 1, corresponding with reductions in LAI and canopy cover.

Overall System Performance

To obtain an overall measure of system performance, the systems were ranked according to several productivity measures and the ranks summed (Tables 8 and 9). By the combined index, the four-crop system ranked only number 5 of 8 in Year 1 and 3 of 5 in Year 2 (1 = highest productivity). By most measures productivity was greatest in successional vegetation in both study years. In both years the maize and sorghum monocultures were more productive than the four-crop system, as were the maize-sorghum and maize-pumpkin systems in Year 1. In both years cowpea and pumpkin monocultures ranked below the four-crop intercrop; in Year 1 the maize-cowpea intercrop was also less productive than the four-crop system.

Table 7. Summary of system productivity measures in Years 1 and 2. Means are given for the Year 2 control plots. Productivity of corresponding monocultures is also given for the four-crop system. Only systems included in both years' experiments are included.

	BIOMASS[a]		EDIBLE BIOMASS[a]		LAI[b]		CANOPY COVER[b]		FULLSTANDEDNESS[c]	
SYSTEM	YEAR 1	YEAR 2	YEAR 1	YEAR 2	YEAR 1	YEAR 2	YEAR 1	YEAR 2	YEAR 1	YEAR 2
MAIZE	249	244	65	62	.81	.54	.43	.36	92	96
SORGHUM	338	352	123	123	.88	.73	.54	.49	88	82
COWPEA	10	20	1	1	.42	.27	.32	.18	48	78
PUMPKIN	112	52	0	26	.74	.39	.64	.29	78	38
FOUR-CROP	228	283	77	67	.74	.63	.49	.36	79	69
CORRESPONDING MONOCULTURES	177	167	47	53	.71	.48	.48	.33	77	74
SUCCESSION	326	271	--	--	2.04	1.40	.83	.73	--	--

[a] at harvest

[b] second LAI/canopy cover sample in Year 2 (day 65); Year 1 LAI/canopy cover linearly interpolated to day 65

[c] third stand count in Year 1 (day 75); Year 2 stand count linearly interpolated to day 75

Table 8. Summary of rankings of systems by various productivity measures, Year 1. Values are rankings of control plot data by each productivity measure. 1=highest value. The succession and sparse maize systems are not included in the rankings, but values in parentheses indicate the rank after which those sytems would have been placed if they had been ranked.

SYSTEM	BIOMASS[a]	DEFOLIATED BIOMASS[b]	EDIBLE BIOMASS[a]	LAI[c]	CANOPY COVER[c]	ROOT BIOMASS[d]	FULLSTAND-EDNESS[e]	SUMMED RANK
SUCCESSION	(2)	(0)	--	(0)	(0)	(1)	--	--
MAIZE-SORGHUM	2	5	2	1	2	5	1	18
MAIZE-PUMPKIN	3	4	4	2	4	2	3	22
SORGHUM	1	7	1	4	3	7	4	27
MAIZE	5	2	6	3	8	4	2	30
SPARSE MAIZE	(2)	(5)	(2)	(2)	(8)	(3)	--	--
FOUR-CROP	6	6	5	5	5	1	5	33
MAIZE-COWPEA	4	1	3	6	7	6	7	34
COWPEA	8	3	8	8	6	3	8	44
PUMPKIN	7	8	7	7	1	8	6	44

[a] at harvest

[b] defoliated plots only

[c] second LAI/canopy cover sample

[d] core method

[e] third stand count

Table 9. Summary of ranking of systems by various productivity measures, Year 2. Values are rankings of systems by each productivity measure (control plots only). 1=highest value. The succession system is not included in the rankings, but values in parentheses indicate the rank after which succession would have been placed if it had been ranked.

SYSTEM	BIOMASS[a]	BIOMASS[b]	DEFOLIATED BIOMASS[c]	EDIBLE BIOMASS[a]	ROOT BIOMASS[b]	LAI[b]	LAI[d]	CANOPY COVER[d]	FULLSTAND-EDNESS[e]	SUMMED RANK
SUCCESSION	(2)	(1)	(0)	--	(0)	--	(0)	(0)	--	--
SORGHUM	1	1	3	3	1	4	1	1	2	17
MAIZE	3	2	2	2	3	1	3	3	1	20
FOUR-CROP	2	3	4	1	2	3	2	2	4	23
PUMPKIN	4	4	5	4	5	2	4	4	5	37
COWPEA	5	5	1	5	4	5	5	5	3	38

[a]at harvest

[b]at flowering

[c]defoliated plots only

[d]second LAI/canopy cover sample

[e]third stand count

Overall Response to the Stress Treatments

The fertilization, pesticide, and watering treatments had differing effects on system productivity, compared with controls, by a variety of measures (Tables 10-12). Fertilization consistently stimulated productivity in all systems, but cowpea and pumpkin monocultures tended to respond less than the other systems. The pesticide treatment increased cowpea productivity by several measures, but had little effect on the productivity of other systems. The watering treatment had no significant effect on cowpea biomass, edible biomass, and fullstandedness compared to controls. Most systems recovered completely from defoliation in both study years. Although few significant differences between defoliated plots and controls were found, cowpea productivity may have been stimulated by defoliation, whereas sorghum and pumpkin did not recover completely from defoliation.

Results: Productivity in Intercrops and Corresponding Monocultures

The first kind of analysis, absolute comparison of productivity differences among systems, does not distinguish between species composition and spatial diversity as possible causes of productivity differences. The finding that sorghum monoculture is more productive than the four-crop intercrop, for example, while interesting from an agronomic standpoint, reveals little or nothing about the effects of diversity on productivity. To evaluate the effects of spatial mixing of crops in fields, each intercrop was compared with an equal area of corresponding monocultures: monocultures of the species comprising the

Table 10. Summary of effects of fertilization on productivity, by system, Year 2. + = significantly higher biomass, root mass, LAI, canopy cover, or fullstandedness in fertilized plots than controls; 0 = no significant difference, by Duncan's tests.

SYSTEM	BIOMASS[a]	BIOMASS[b]	EDIBLE BIOMASS[a]	ROOT BIOMASS[b]	LAI[b]	LAI[c]	CANOPY COVER[c]	FULLSTAND-EDNESS[d]
MAIZE	+	+	+	+	+	+	+	0
SORGHUM	+	+	0	+	+	0	0	0
COWPEA	0	0	0	0	+	+	+	0
PUMPKIN	+	0	+	0	+	0	0	0
FOUR-CROP	+	+	+	+	+	0	+	0
SUCCESSION	+	+		0	+	+	0	

[a] at harvest

[b] at flowering

[c] second LAI/canopy cover sample

[d] third stand count

Table 11. Summary of effects of pesticide spraying on productivity, by system, Year 2. + = significantly higher biomass, LAI, canopy cover, or fullstandedness in sprayed plots than controls; - = significantly lower in sprayed plots than controls; 0 = no significant difference, by Duncan's tests.

SYSTEM	BIOMASS[a]	EDIBLE BIOMASS[a]	LAI[b]	CANOPY COVER[b]	FULLSTAND-EDNESS[c]
MAIZE	0	0	0	0	0
SORGHUM	0	0	0	0	0
COWPEA	0	0	+	+	+
PUMPKIN	0	0	0	-	-
FOUR-CROP	0	0	0	+	0
SUCCESSION	0	0	0	0	

[a]at harvest

[b]at flowering

[c]third stand count

Table 12. Summary of effects of defoliation on productivity, by system, Years 1 and 2. – = significantly lower biomass or fullstandedness in defoliated than control plots; 0 = no significant difference, by Duncan's tests.

SYSTEM	YEAR	BIOMASS[a]	EDIBLE BIOMASS[a]	FULLSTAND-EDNESS[b]
MAIZE	1	0	0	
	2	0	0	0
SPARSE MAIZE	1	0	0	
SORGHUM	1	0	0	
	2	0	0	0
COWPEA	1	0	0	
	2	0	0	0
PUMPKIN	1	0	0	
	2	0	0	–
MAIZE-SORGHUM	1	0	0	
MAIZE-COWPEA	1	0	0	
MAIZE-PUMPKIN	1	–	0	
FOUR-CROP	1	0	0	
	2	0	0	0
SUCCESSION	1	0	0	
	2	0	0	0

[a]at harvest

[b]third stand count

intercrop. A given area (1 ha, for example) was divided among the intercrops in the same proportion as the species were planted in the intercrop. The difference between an absolute yield comparison and a comparison with corresponding monocultures is shown diagrammatically in Figure 34 (numbers 1 and 2).

The comparison of intercrops with corresponding monocultures may also be expressed as the Yield Equivalent Ratio (YER) of the intercrop (Figure 34, number 3), or as a histogram of two bars, the first of which represents the yield in intercrop and the second, yield from the same area divided among corresponding monocultures (Figure 34, number 4). The first bar equals the numerator of YER; the second, the denominator. Significance of difference between the two bars (or between the numerator and denominator of YER) was tested with the SAS Contrast Procedure.

Edible and Total Aboveground Biomass at Harvest

Intercrop systems yielded more than corresponding monocultures in control plots of all systems in both years (Figures 35 and 36). This was due primarily to the greater yield of maize in intercrop than in monoculture. The intercrop advantage in terms of edible and total yield was significant in the Year 1 maize-pumpkin and maize-cowpea systems and the Year 2 four-crop system.

Intercrop systems were also consistently more productive than corresponding monocultures in the stress treatments (Figures 37-40). Edible and total yields of the Year 1 maize-pumpkin, maize-cowpea, and four-crop systems were significantly greater than their corresponding monocultures for a sample of control and defoliated treatments combined (Figures 37 and 38). Test results for each treatment tested separately

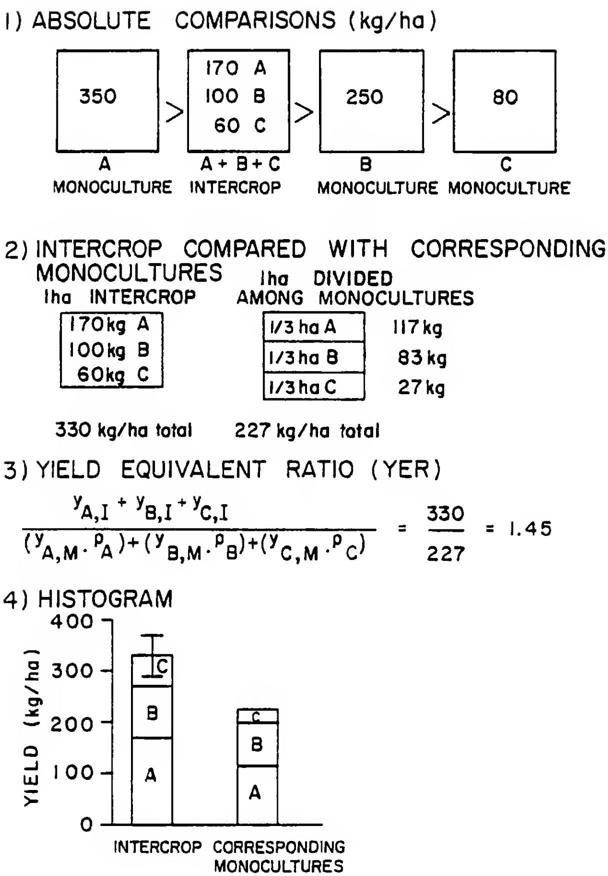

Figure 34. Four ways of comparing intercrops with monocultures (a hypothetical example). Species A, B, and C are each planted at one-third full stand densities in the intercrop ($p_a = p_b = p_c = .33$). In the equation for YER, $Y_{i,I}$ is the yield of species i in intercrop, $Y_{i,M}$ is the yield of species i in monoculture, and p_i is the proportion of a full stand of species i planted in the intercrop. In the histogram, standard deviations cannot be calculated for corresponding monocultures unless they are paired in the experimental design. Methods 2, 3, and 4 are mathematically identical.

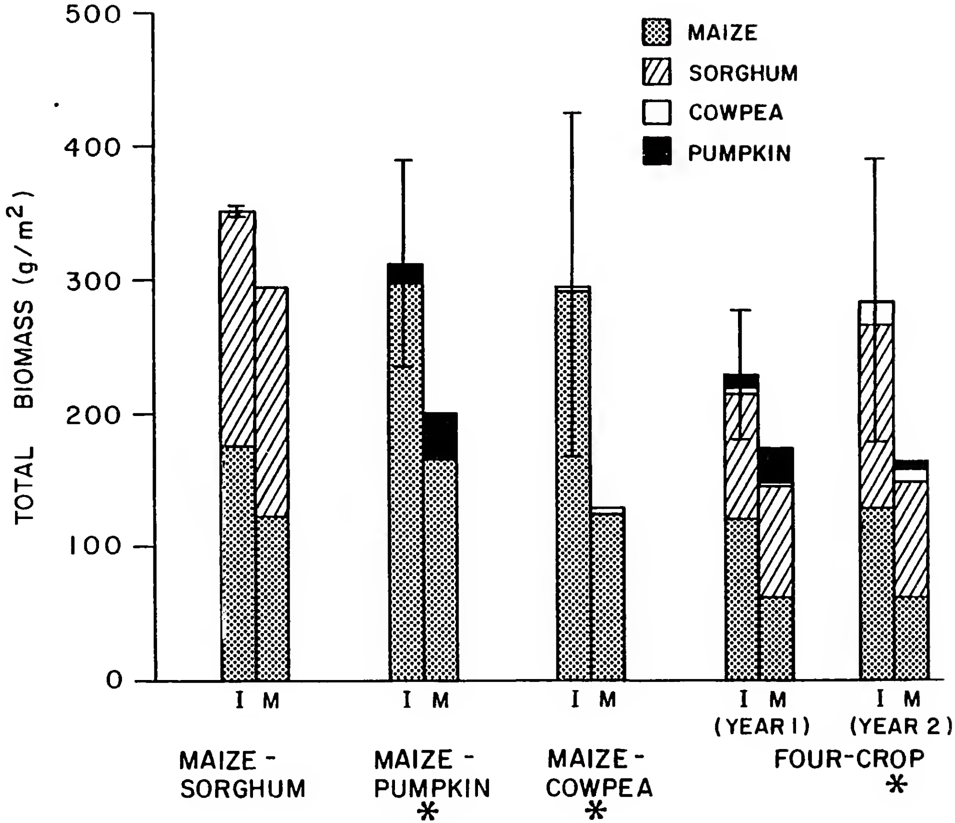

Figure 35. Comparisons of total aboveground biomass in intercrops and corresponding monocultures in the control treatment, Years 1 and 2. I = intercrop; M = corresponding monocultures. Intercrop and monoculture yields are significantly different in pairs of bars marked with an asterisk, by SAS Contrast procedure, performed on samples of all treatments combined (not shown in the graph).

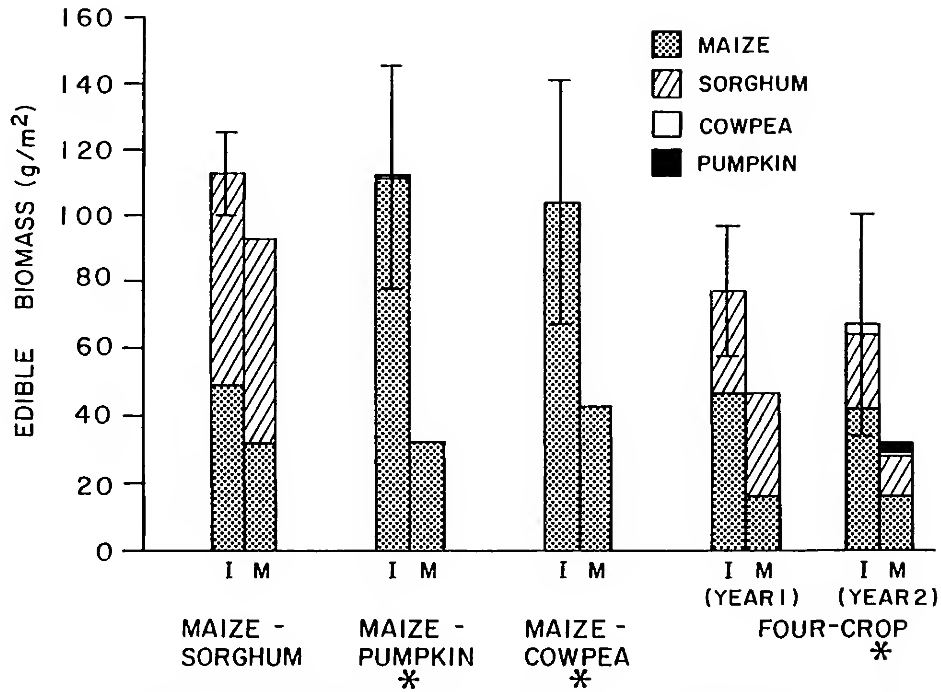

Figure 36. Comparisons of edible biomass in intercrops and corresponding monocultures in the control treatment, Years 1 and 2. I = intercrop; M = corresponding monocultures. Intercrop and monoculture yields are significantly different in pairs of bars marked with an asterisk, by SAS Contrast procedure, performed on samples of all treatments combined (not shown in the graph).

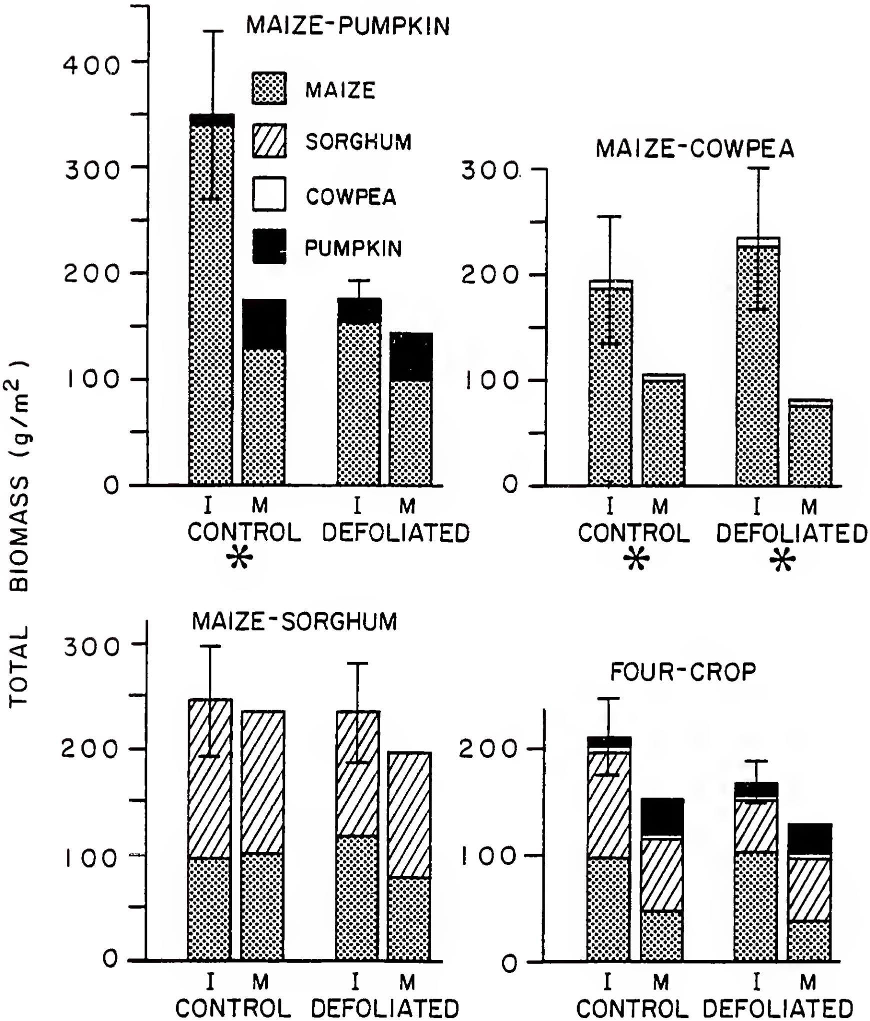

Figure 37. Comparison of total aboveground biomass in intercrops and corresponding monocultures in the control and defoliated treatments, Year 1. I = intercrop; M = corresponding monocultures. Intercrop yielded significantly more than corresponding monocultures (SAS Contrast procedure, performed on a sample of control and defoliated treatments combined) in the maize-pumpkin, maize-cowpea, and four-crop systems. Significant intercrop/monoculture differences when tested by-treatment are indicated with an asterisk.

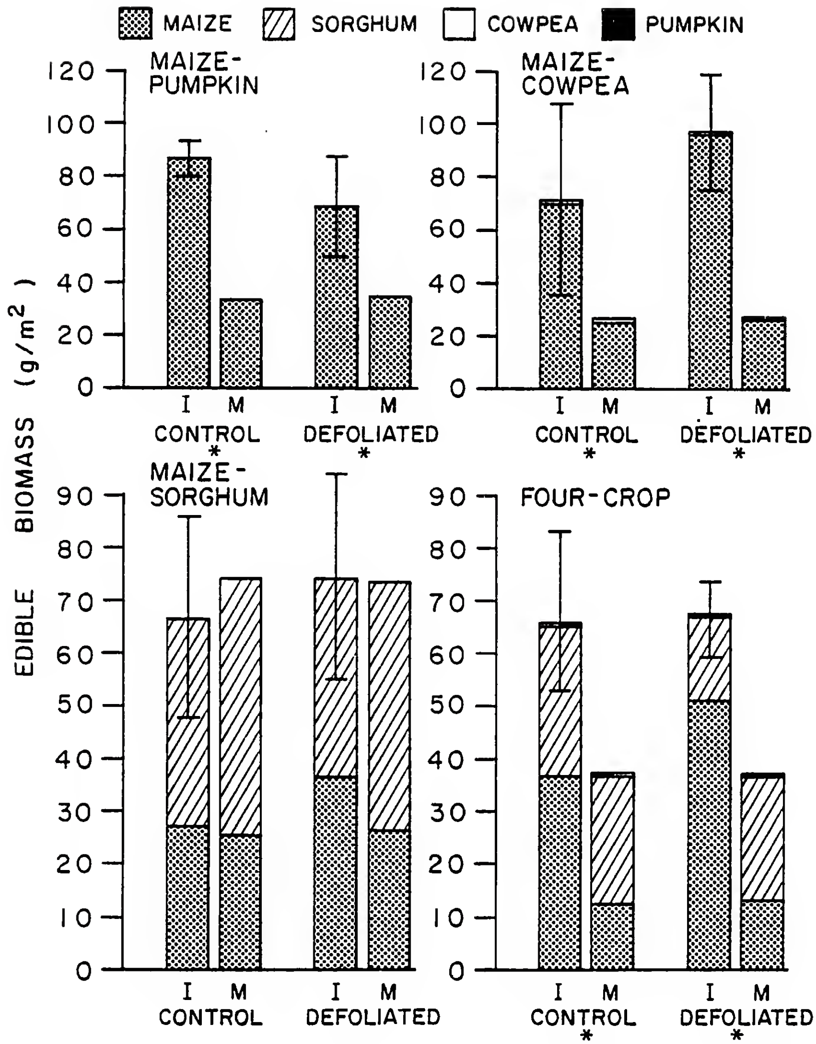

Figure 38. Comparison of edible biomass in intercrop and corresponding monocultures in the control and defoliated treatments, Year 1. I = intercrop; M = corresponding monocultures. Intercrop yielded significantly more than corresponding monocultures (SAS Contrast procedure, performed on a sample of control and defoliated treatments combined) in the maize-pumpkin, maize-cowpea, and four-crop systems. Significant intercrop/monoculture differences when tested by-treatment are indicated with an asterisk.

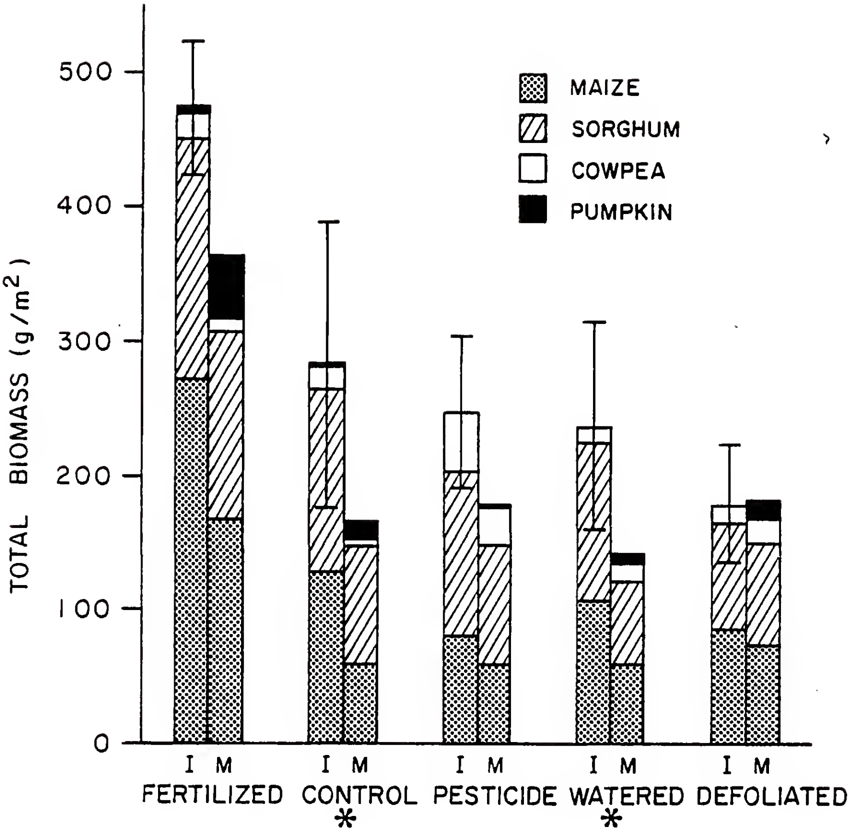

Figure 39. Comparison of total aboveground biomass in intercrops and corresponding monocultures in five treatments, Year 2. I = intercrop; M = corresponding monocultures. Intercrop biomass was significantly higher than that of corresponding monocultures by SAS Contrast procedure, performed on a sample of all treatments combined. Significant intercrop/monoculture differences when tested by-treatment are indicated with asterisks.

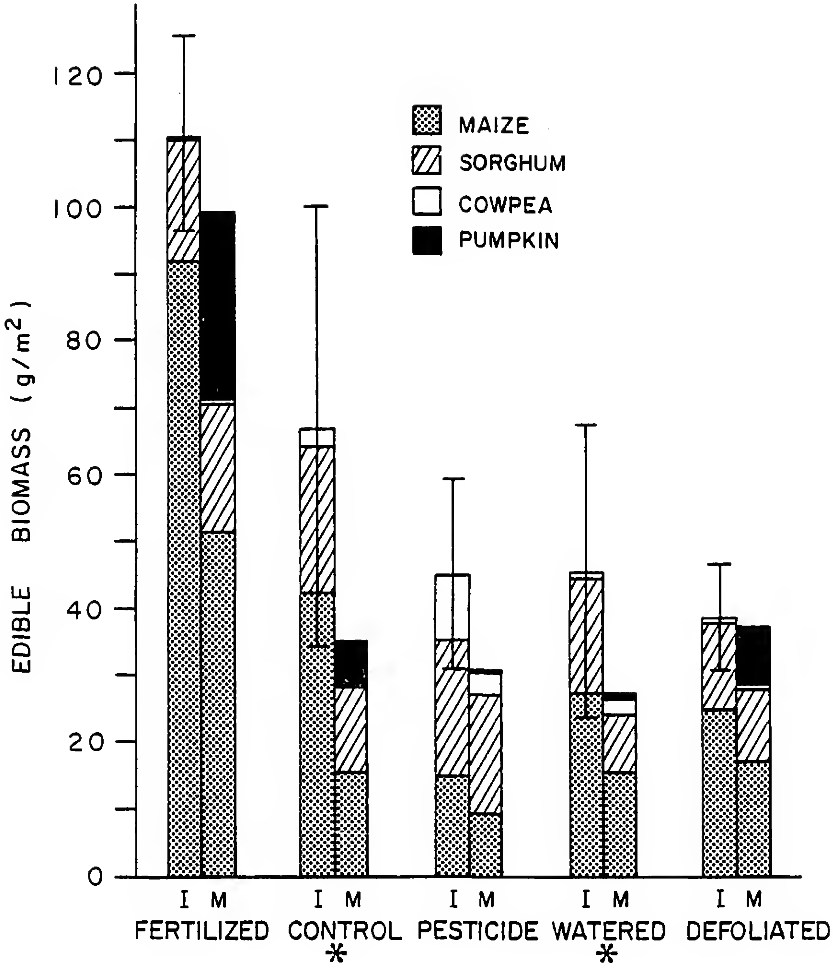

Figure 40. Comparisons of edible biomass in intercrops and corresponding monocultures in five treatments, Year 2. I = four-crop intercrop; M = corresponding monocultures. Intercrop edible biomass was significantly higher than that of corresponding monocultures by SAS Contrast procedure, performed on a sample of all treatments combined. Significant intercrop/monoculture differences when tested by-treatment are indicated with asterisks.

are given in the figure. In Year 2, both edible and total biomass was significantly higher in the four-crop system than in corresponding monocultures for a sample of all treatments combined (Figures 39 and 40). When tested by treatment, the intercrop/monoculture difference was significant only in the control and watered treatments. The intercrop advantage (in terms of both edible and total yield) was lowest in the defoliated treatment in Year 2 due to the negative response of maize and sorghum to defoliation in the four-crop system.

LAI and Canopy Cover

LAI and canopy cover were consistently higher in intercrop systems than in corresponding monocultures for all systems and treatments in both years, but no significant intercrop/monoculture differences were found (Figure 41).

Leaf Mass at Defoliation

Defoliated leaf mass was slightly (nonsignificantly) lower in the intercrops than in corresponding monocultures in all systems except maize-cowpea, where intercrop defoliated biomass slightly (nonsignificantly) exceeded that in the monocultures.

Root Biomass, Year 1

Root biomass (0-40 cm) was higher in the maize-sorghum, maize-pumpkin, and four-crop intercrop systems than in their corresponding monocultures, but was lower in the maize-cowpea intercrop than in corresponding monocultures; none of the differences were significant.

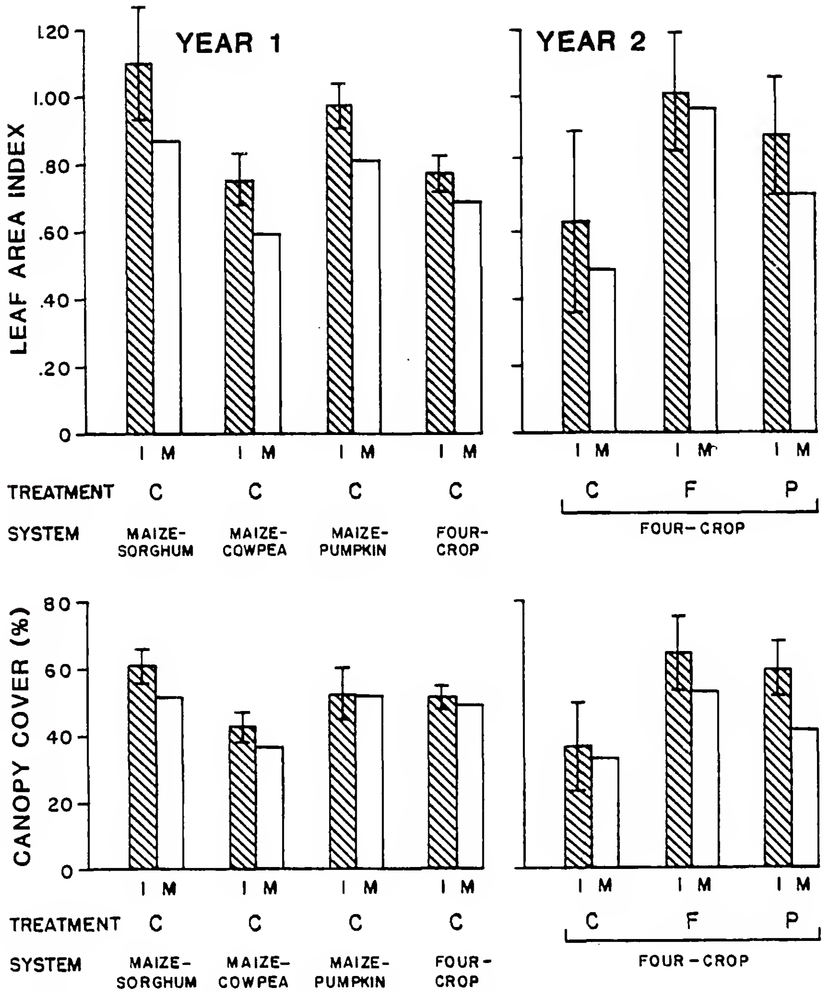

Figure 41. Comparisons of LAI and canopy cover in intercrops and corresponding monocultures, Years 1 and 2. Data are from sample 3 in Year 1 and sample 2 in Year 2 (the samples most representative of overall leaf area and canopy cover development). I = intercrop (hatched bars); M = corresponding monocultures (open bars); C = control treatment; F = fertilized; P = pesticide. No intercrop/monoculture differences were significant by SAS Contrast procedure.

Table 13. Root biomass, total aboveground biomass, and LAI at flowering in intercrops and corresponding monocultures, Year 2. Entries are $\bar{x} \pm s$ (in g/m^2 for root and total biomass, unitless for LAI). None of the intercrop/monoculture differences were significant by SAS Contrast procedure.

	CONTROL		FERTILIZED	
	FOUR-CROP	CORRESPONDING MONOCULTURES	FOUR-CROP	CORRESPONDING MONOCULTURES
ROOT BIOMASS	10.88 ± 4.34	9.27	28.87 ± 3.47	22.85
TOTAL ABOVEGROUND BIOMASS	144.47 ± 68.28	124.70	295.5 ± 17.08	274.96
LAI	.59 ± .52	.52	1.12 ± .15	1.04

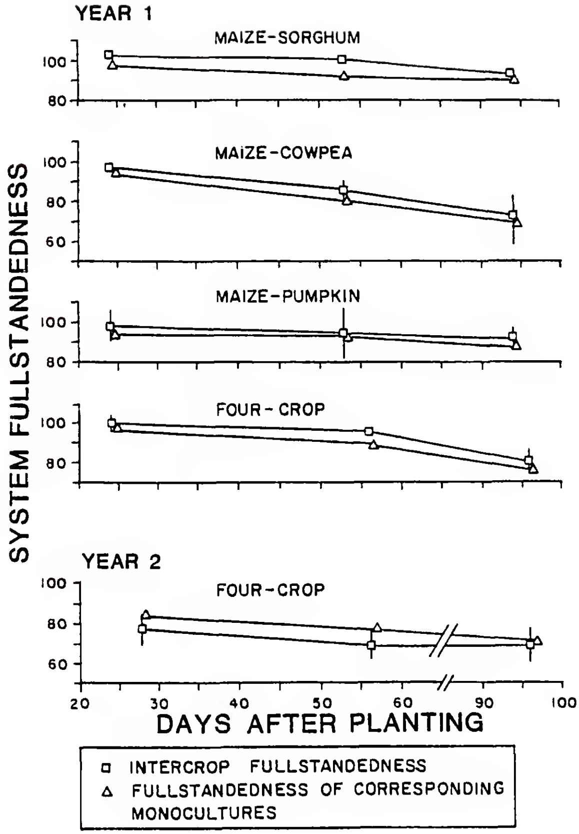

Figure 42. Fullstandedness of intercrops and corresponding monocultures in the control treatment, Years 1 and 2. Tests for significant intercrop/monoculture differences (SAS Contrast procedure) were performed on a sample of all treatments combined (not shown in the graph) except in sample 3, Year 2, which was analyzed by-treatment because of significant interaction. The only significant intercrop/monoculture difference found was in the sample 2, Year 2 four-crop system, which was significantly less full than corresponding monocultures.

Table 14. Intercrop yield advantage (YER), Years 1 and 2. Values are YER based on each of the given productivity measures (control plots only). Asterisks indicate YERs in which numerator and denominator are significantly different by SAS Contrast procedure.

SYSTEM	BIOMASS[a]	BIOMASS[b]	DEFOLIATED BIOMASS[c]	EDIBLE BIOMASS[a]	ROOT BIOMASS[d]	ROOT BIOMASS[b]	LAI[b]	LAI[e]	CANOPY COVER[e]
YEAR 1									
MAIZE-SORGHUM	1.19		.79	1.22	1.88			1.26	1.20
MAIZE-COWPEA	2.27*		1.19	2.79*	.60			1.31	1.17
MAIZE-PUMPKIN	1.57*		.89	3.47*	2.92			1.20	1.01
FOUR-CROP	1.31		.87	1.64	7.94			1.12	1.04
YEAR 2									
FOUR-CROP	1.72*	1.16	.75	2.03*		1.17	1.06	1.27	1.10

[a] at harvest
[b] at flowering
[c] defoliated plots only
[d] core method, Year 1
[e] second LAI/canopy cover sample

Aboveground Biomass, LAI, and Root Biomass at Flowering, Year 2

The four-crop system had greater aboveground biomass, root biomass (0-15 cm), and LAI at flowering than corresponding monocultures in both the control and fertilization treatments (Table 13); the differences were not significant.

Fullstandedness

Intercrop systems tended to have slightly (nonsignificantly) fuller stands than their corresponding monocultures, with the exception of the Year 2, sample 2 four-crop system, which was significantly less full than corresponding monocultures (Figure 42). The stress treatments had little effect on fullstandedness; the only significant difference was the defoliated four-crop system (Year 2, sample 3 only), which was significantly less full than corresponding monocultures due to high maize mortality.

Yield Equivalent Ratios (YERs)

Despite the seemingly poor performance of the intercrop system on an absolute scale, the diverse systems were consistently more productive than their simple counterparts, as shown by the preponderance of YERs above one for various productivity measures (Table 14). Only YERs based on defoliated biomass did not conform to this generalization, possibly because the productivity advantage of intercropping was difficult to detect so early in the growing season. Two other minor deviations from the generalization of greater productivity in diverse systems were greater root biomass (by the core method) in monocultures

than in the maize-cowpea system, and slightly higher fullstandedness in monocultures than in the four-crop system in one sample.

Fertilization, pesticide spraying, and defoliation in Year 2 reduced four-crop YER (compared to that of controls, Table 15); watering had no effect. The intercrop yield advantage was lowest in the defoliated treatment in Year 2, and also in the Year 1 maize-pumpkin system. Defoliation increased YER in the maize-cowpea system, however, and had little effect on YER in the Year 1 four-crop and maize-sorghum systems.

Results: Productivity of Species from System to System

Introduction

Each species' performance in simple and diverse systems was evaluated by comparing various productivity measures, adjusted to compensate for the reduced planting density of the species in the intercrop. This adjustment allows one to draw conclusions about whether a species' productivity in an intercrop is higher or lower than expected based on the proportion of a full stand planted and the species' yield in monoculture. To compare intercrop and monoculture yields of a given species, density-adjusted productivity is calculated by dividing the intercrop yield by the proportion of a full stand of that species planted in the intercrop. For example, maize adjusted total biomass equals $2 \cdot (g/m^2$ harvested) for the maize-sorghum, maize-cowpea, and sparse maize systems; $1.5 \cdot (g/m^2$ harvested) for the maize-pumpkin

Table 15. Effects of stress treatments on intercrop yield advantage (YER), Years 1 and 2. Yield Equivalent Ratios (YERs) are based on edible and total biomass at harvest. Asterisks indicated YERs in which the numerator and denominator are significantly different by SAS Contrast procedure.

			YIELD EQUIVALENT RATIO (YER)	
YEAR	SYSTEM	TREATMENT	BIOMASS	EDIBLE BIOMASS
1	MAIZE-SORGHUM	CONTROL	1.19	1.22
		DEFOLIATED	1.21	1.01
1	MAIZE-COWPEA	CONTROL	2.27*	2.79*
		DEFOLIATED	2.76*	3.37*
1	MAIZE-PUMPKIN	CONTROL	1.57*	3.47*
		DEFOLIATED	1.25	2.00*
1	FOUR-CROP	CONTROL	1.31	1.64
		DEFOLIATED	1.30	1.80*
2	FOUR-CROP	CONTROL	1.72*	2.03*
		FERTILIZED	1.24	1.12
		PESTICIDE	1.37	1.32
		DEFOLIATED	.99	1.04
		WATERED	1.66*	1.64*

system; and $4 \cdot (g/m^2$ harvested) for the four-crop system (division by 1/2, 2/3, and 1/4, respectively). The adjustment factor is 1.0 for recommended-density monocultures, so adjusted yield equals unadjusted yield.

Several variables were expressed on a per-plant basis; these corresponded approximately with the density-adjusted variables. They were not identical, however, since the number of surviving plants was different than the planting density used to calculate density-adjusted variables. Only the density-adjusted variables were reported here because they are more indicative of a species' function in the ecosystem. In general, the two types of variables matched in terms of order and significance of differences among systems and treatments. Per-plant edible and total biomass, maize cobs/plant, and sorghum heads/plant agreed with the corresponding density-adjusted variables (adjusted edible and total biomass, adjusted cob production, and adjusted head production) except for occasional minor differences in the significance tests (without changes in order) or changes in order (without changes in significance).

For simplicity, successional monocots and successional dicots are referred to as "species" in this section; their performance was evaluated only in the succession system, and no adjustments for density were made.

Productivity measures were again divided into measures of biomass accretion ("direct" measures) and measures of biomass distribution ("indirect" measures).

In this section, differences in each species' performance in various systems and in the stress treatments are evaluated by a number

of direct and indirect productivity measures; correlations among the measures are examined; year-to-year productivity differences are summarized; system-to-system differences in each species' performance are summarized; and the effects of the stress treatments on each species are summarized.

Measures of Biomass Accretion

Edible and total aboveground biomass at harvest

Maize edible and total biomass were lowest in maize monoculture and maize-sorghum intercrop and highest in sparse maize monoculture and maize-cowpea intercrop when adjusted for planting density (Figure 43). In both years, both edible and total maize biomass were significantly higher in the four-crop system than in monoculture. Sorghum total biomass (adjusted for planting density, Figure 44) was significantly higher in the four-crop system than in monoculture in Year 2; other differences were not statistically significant. However, both edible and total sorghum biomass were consistently higher in the maize-sorghum and four-crop systems than in sorghum monoculture. Cowpea edible and total biomass (Figure 45) were significantly higher in the four-crop intercrop than in cowpea monoculture in Year 2. In Year 1 edible and total cowpea biomass were very low in all cowpea systems, and no significant differences among systems were found. Pumpkin edible and total biomass (Figure 46) were consistently much higher in pumpkin monoculture than in the maize-pumpkin and four-crop systems, but the differences were significant only for Year 1 total biomass. The low

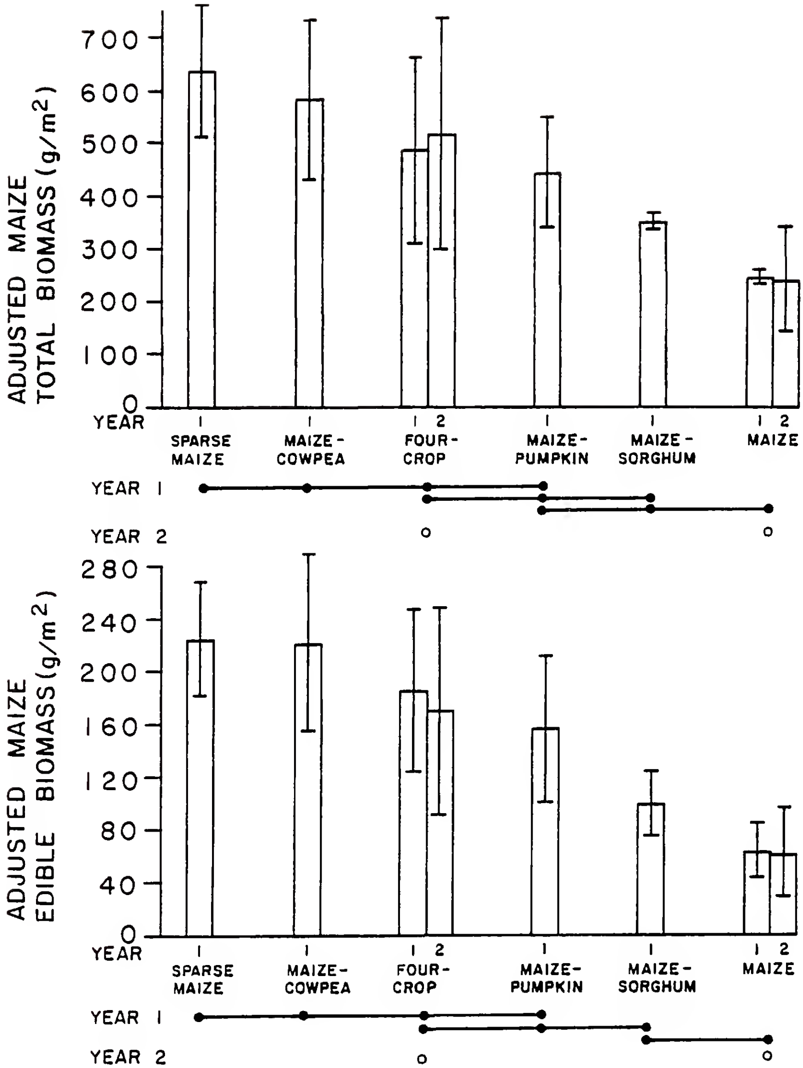

Figure 43. Density-adjusted maize total aboveground biomass and edible biomass in the control treatment, Years 1 and 2. Systems not connected by a common line are significantly different by Duncan's tests. Solid dots are Year 1; open dots, Year 2.

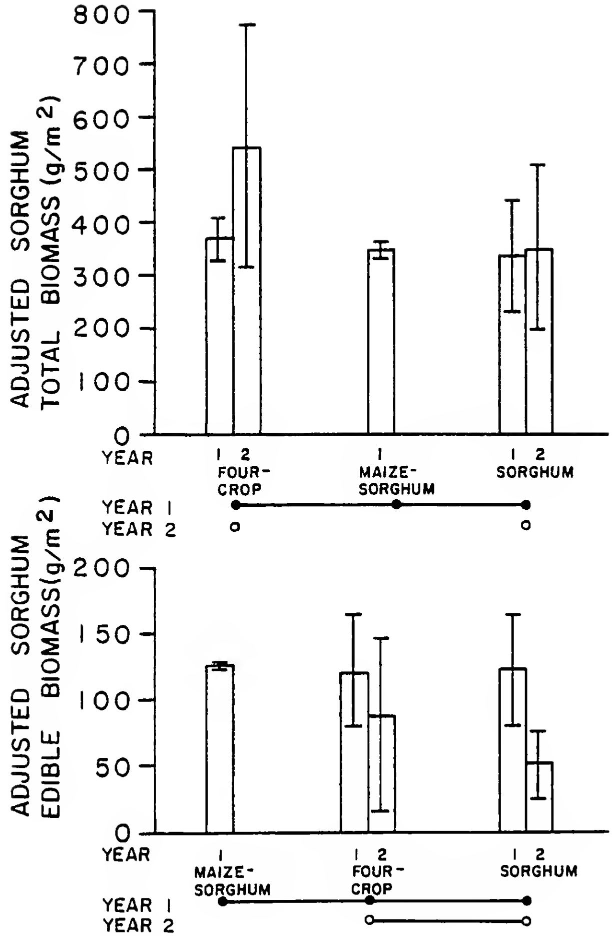

Figure 44. Density-adjusted sorghum total aboveground biomass and edible biomass in the control treatment, Years 1 and 2. Systems not connected by a common line are significantly different by Duncan's tests. Year 2 tests were based on samples of all treatments combined (not shown in the graph). Solid dots are Year 1; open dots, Year 2.

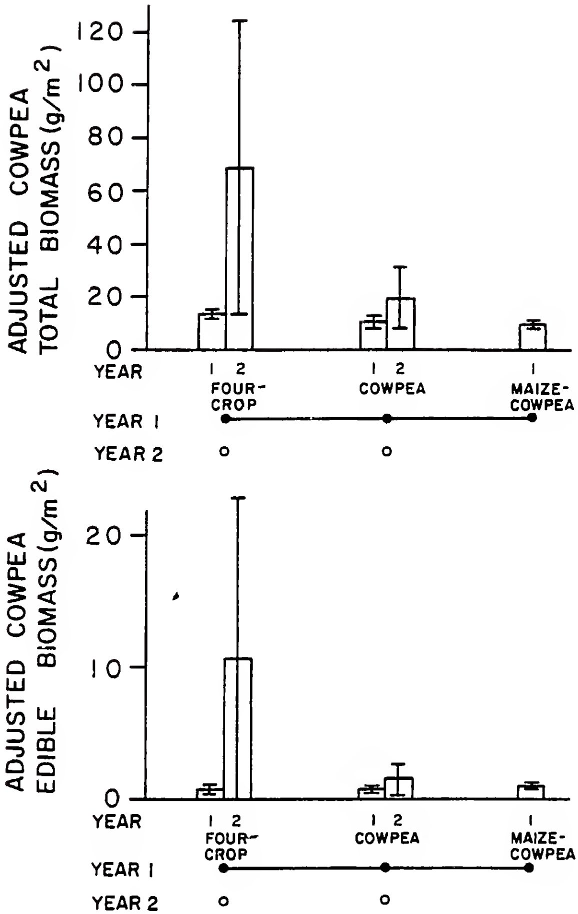

Figure 45. Density-adjusted cowpea total aboveground biomass and edible biomass in the control treatment, Years 1 and 2. Systems not connected by a common line are significantly different by Duncan's tests. Solid dots are Year 1; open dots, Year 2.

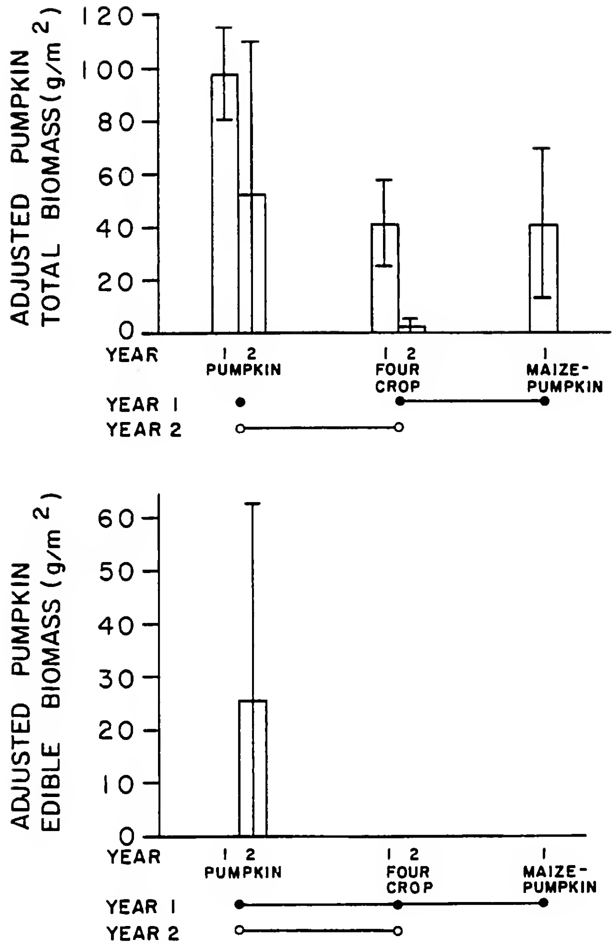

Figure 46. Density-adjusted pumpkin total aboveground biomass and edible biomass in the control treatment, Years 1 and 2. Systems not connected by a common line are significantly different by Duncan's tests. Solid dots are Year 1; open dots, Year 2.

degree of significance for the other comparisions was due to high plot-to-plot variation.

Effects of stress treatments on edible and total yield of each crop species, and monocot and dicot components of the successional system, areshown in Figures 47-55. Maize yield was not significantly affected by defoliation in Year 1 (Figure 47); maize edible and total biomass increased with defoliation in the maize-sorghum, maize-cowpea, and four-crop systems and decreased in the maize-pumpkin and maize monoculture systems. In Year 2, edible and total maize biomass were reduced by defoliation in the four-crop system and increased by defoliation in monoculture (Figure 48), but these differences were not significant. Fertilization significantly increased both edible and total maize biomass in both the four-crop and maize monoculture systems; the watering treatment had no significant effect on either variable in either system. Pesticide spraying was slightly deleterious to maize in both the four-crop system and monoculture, when compared with controls. Maize yield (both edible and total) was significantly higher in the four-crop system than in monoculture in the two highest-yielding treatments (control and fertilization), but not in the three lowest-yielding treatments (watering, defoliation, and pesticide).

Sorghum was slightly negatively affected by defoliation; defoliation significantly reduced sorghum total biomass in the four-crop system. Non-significant decreases in sorghum edible biomass in the four-crop system and total biomass in the maize-sorghum and sorghum monoculture systems also accompanied defoliation in Year 1 (Figure 49). In Year 2 (Figure 50), sorghum edible and total yield were significantly lower in defoliated than control plots (tested for a sample of four-crop and sorghum

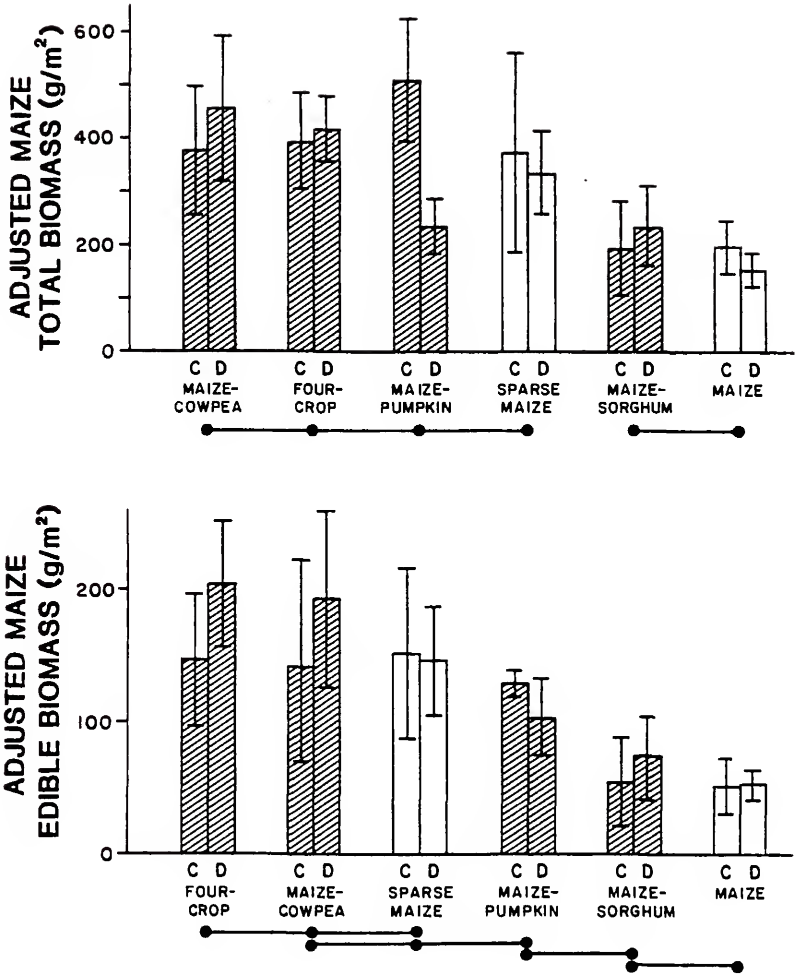

Figure 47. Density-adjusted maize total aboveground biomass and edible biomass in the control (C) and defoliated (D) treatments, Year 1. Hatched bars are intercrop systems; open bars are monocultures. Systems not connected by a common line are significantly different by Duncan's tests, performed on samples of both treatments combined. Differences between control and defoliated plots were not significant for either variable by Duncan's tests, performed on samples of all systems combined.

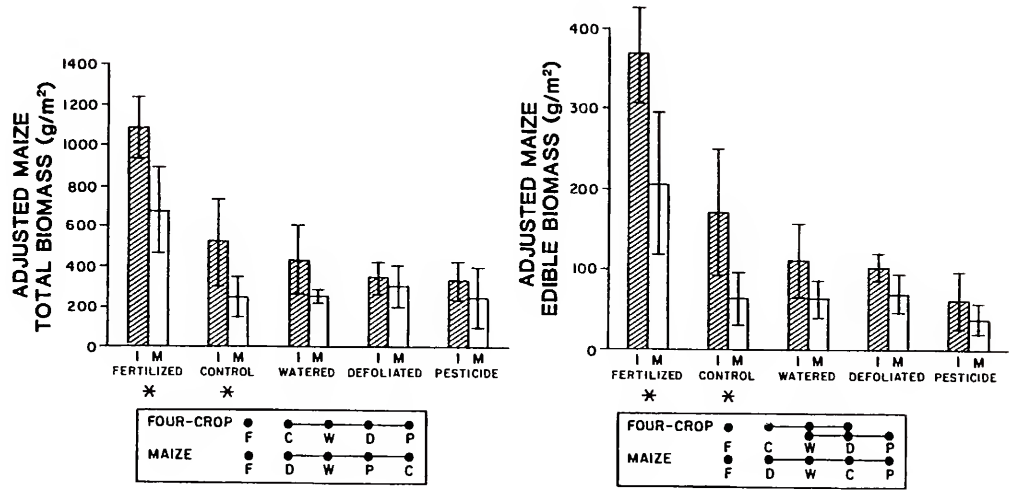

Figure 48. Density-adjusted maize total aboveground biomass and edible biomass in five treatments, Year 2. I = four-crop intercrop (hatched bars); M = maize monoculture (open bars). C = control treatment, F = fertilized, P = pesticide, D = defoliated, W = watered. Significant differences between intercrops and monocultures are indicated with an asterisk, and treatments not connected by a common line are significantly different (by Duncan's tests).

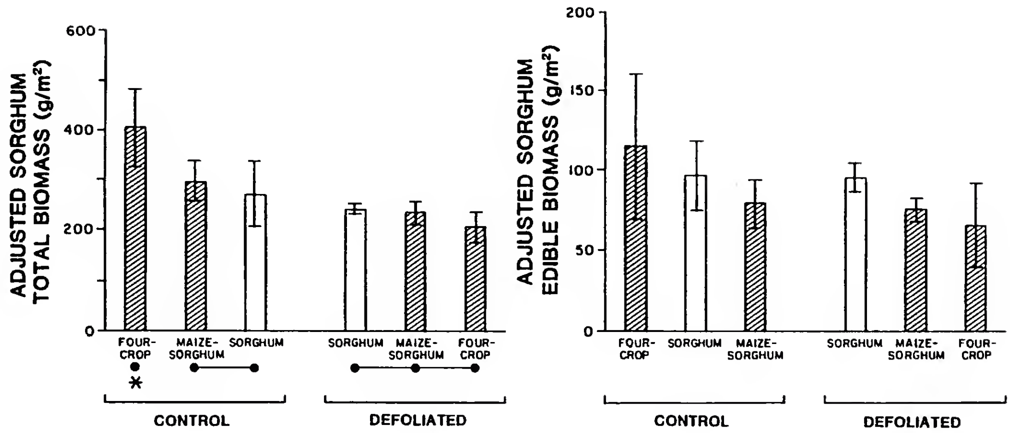

Figure 49. Density-adjusted sorghum total aboveground biomass and edible biomass in the control and defoliated treatments, Year 1. Hatched bars are intercrop systems; open bars are monocultures. Duncan's tests were performed separately for each system and treatment for total biomass, but were performed on samples of all systems or treatments combined for edible biomass. For total biomass, asterisks indicate significant differences between control and defoliated treatments; systems not connected with a common line are significantly different. No significant differences in edible biomass were found among systems or treatments.

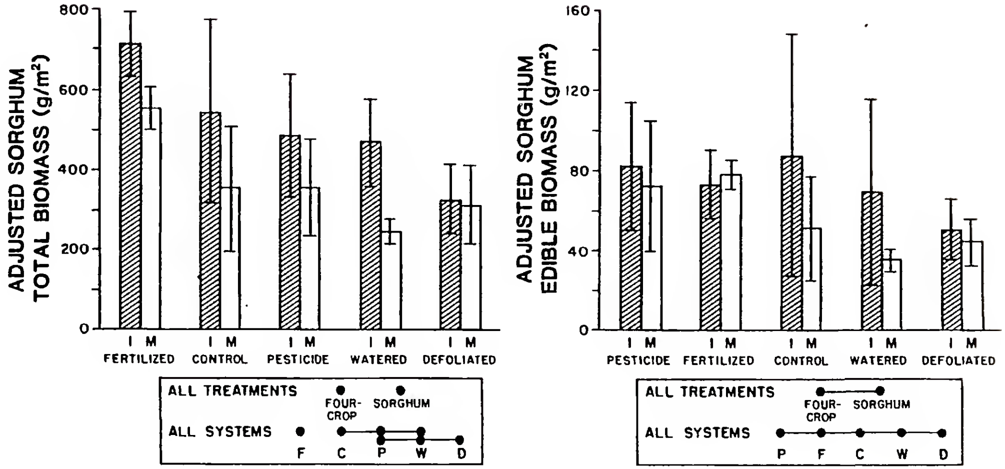

Figure 50. Density-adjusted sorghum total aboveground biomass and edible biomass in five treatments, Year 2. I = four-crop intercrop (hatched bars); M = sorghum monoculture (open bars). C = control treatment, F = fertilized, P = pesticide, D = defoliated, W = watered. Systems or treatments not connected by a common line are significantly different by Duncan's tests, performed on samples of all systems or treatments combined.

monoculture system combined), but the greatest reduction occurred in the four-crop system. Fertilization significantly increased sorghum total biomass, but not edible biomass, compared with totals. The greatest difference between four-crop and monoculture sorghum yield occurred in the control and watered plots. In the Year 2 defoliated plots the difference between sorghum total biomass in intercrop and monoculture was negligible, and sorghum edible biomass was slightly higher in monoculture than in the four-crop system in the fertilization treatment.

Defoliation decreased cowpea edible and total biomass in the intercrop systems and increased or had no effect on yield in the cowpea monoculture in both years (Figures 51 and 52); the differences were not significant, however. Pesticide spraying significantly increased yield compared with controls. Fertilization increased cowpea total biomass and decreased edible biomass (both nonsignificantly) in both the four-crop and cowpea monoculture systems. Watering tended to decrease cowpea edible and total yield in the four-crop system and increase it in the cowpea monoculture, but the only significant difference was increased edible biomass in the watered cowpea monoculture. In Year 2, cowpea total biomass was significantly higher in the four-crop system than in the cowpea monoculture in the three highest-yielding treatments (pesticide, fertilization, and control), but was higher in monoculture in the defoliation and watering treatments. Edible cowpea biomass was significantly higher in the four-crop intercrop than in the cowpea monoculture in the two highest-yielding treatments (pesticide and control), nonsignificantly higher in intercrop in the fertilization

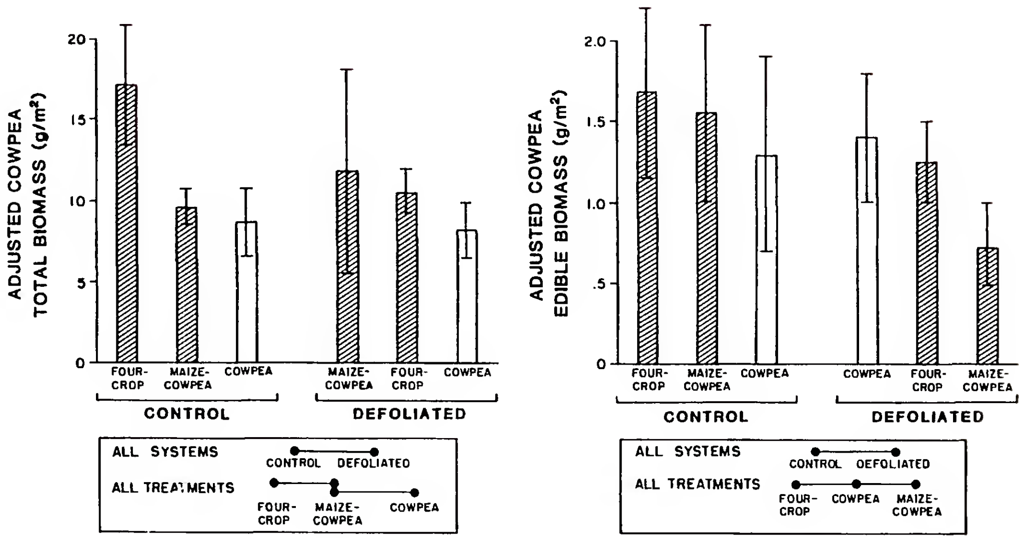

Figure 51. Density-adjusted cowpea total aboveground biomass and edible biomass in control and defoliated treatments, Year 1. Hatched bars are intercrops; open bars are monocultures. Systems or treatments not connected by a common line are significantly different by Duncan's tests, performed on samples of all systems or treatments combined.

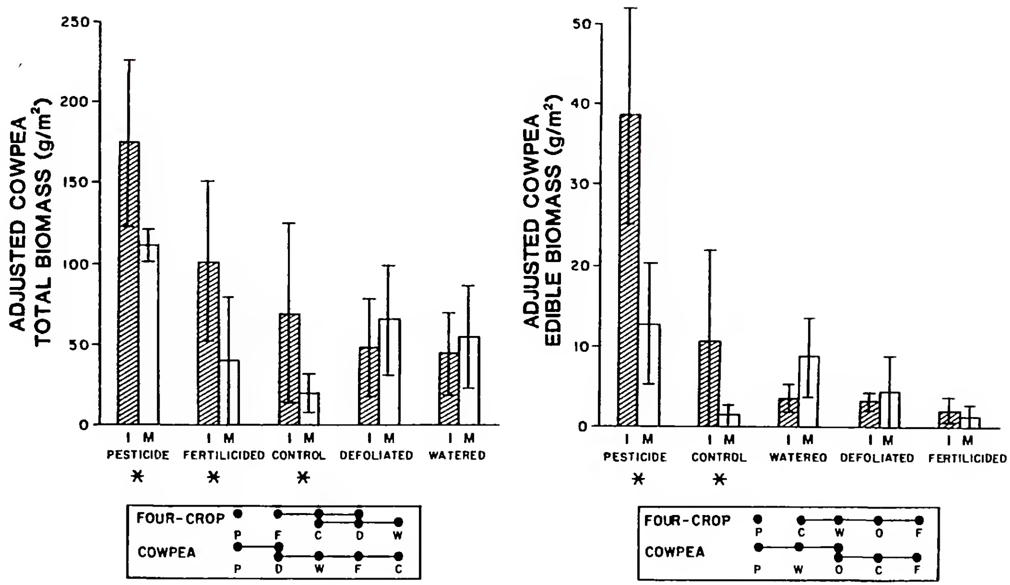

Figure 52. Density-adjusted cowpea total aboveground biomass and edible biomass in five treatments, Year 2. I = four-crop intercrop (hatched bars); M = cowpea monoculture (open bars). C = control treatment, F = fertilized, P = pesticide, D = defoliated, W = watered. Significant differences between intercrops and monocultures are indicated with an asterisk, and treatments not connected by a common line are significantly different (by Duncan's tests).

treatment, and higher in monoculture in the defoliation and watering treatments.

Defoliation had no significant effect on pumpkin edible or total biomass in either study year (Figures 53 and 54). In Year 2, fertilization significantly increased both edible and total pumpkin yield in the pumpkin monoculture and nonsignificantly increased total biomass in the four-crop system. (Edible biomass in the four-crop system was zero.) Both the watering and pesticide treatments decreased edible and total pumpkin yields in both the four-crop and pumpkin monoculture systems. In Year 2, edible and total pumpkin biomass were consistently much higher in pumpkin monoculture than in the four-crop system, but due to high plot-to-plot variability, the difference was only significant for the highest yielding (fertilization) treatment.

The ordering of systems by total and edible biomass of each crop species was the same in the Year 1 small control and defoliated plots and in the Year 1 main plots.

Total biomass of successional vegetation and its monocot/dicot composition was approximately the same in defoliated and control plots in Year 1 (Figure 55). In Year 2, when defoliation was performed later in the growing season, total biomass was greater in defoliated than control plots and contained a greater percent of dicots, but these differences were not significant. Defoliation increased dicot biomass by approximately 100 g/m^2 in Year 2, but did not affect monocot biomass. Fertilization significantly increased total successional biomass and monocot biomass, and caused a slight decline in dicot biomass. Pesticide spraying increased total biomass, monocot biomass, and dicot biomass, but not significantly. The watering treatment had no significant effect on

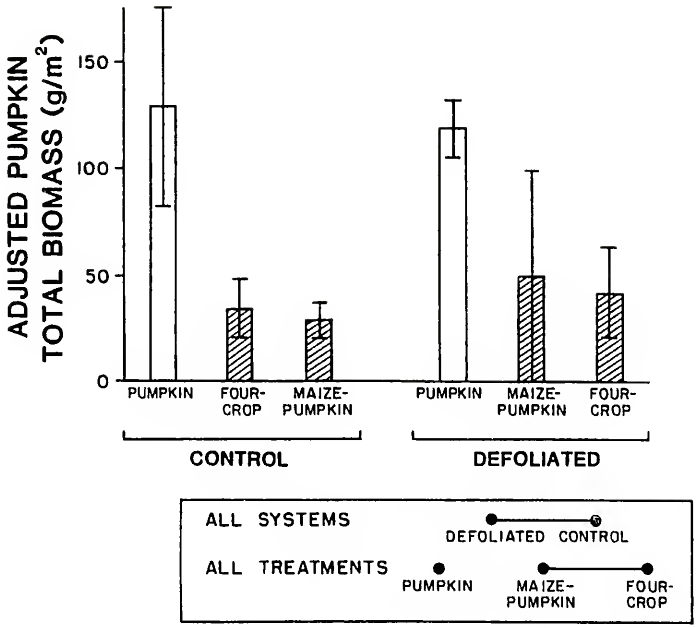

Figure 53. Density-adjusted pumpkin total aboveground biomass in the control and defoliated treatments, Year 1. Hatched bars are intercrops; open bars are monocultures. Systems or treatments not connected by a common line are significantly different by Duncan's tests, performed on samples of all systems or treatments combined. Edible yield was zero in all plots in Year 1.

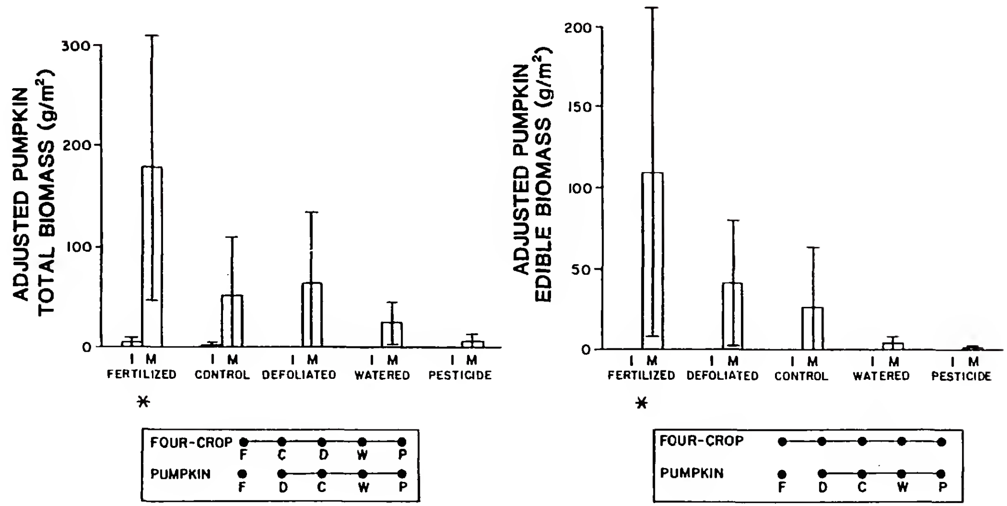

Figure 54. Density-adjusted pumpkin total aboveground biomass and edible biomass in five treatments, Year 2. I = four-crop intercrop (hatched bars), M = pumpkin monoculture (open bars). C = control treatment, F = fertilized, P = pesticide, D = defoliated, W = watered. Significant differences between intercrops and monocultures are indicated with an asterisk, and treatments not connected by a common line are significantly different (by Duncan's tests).

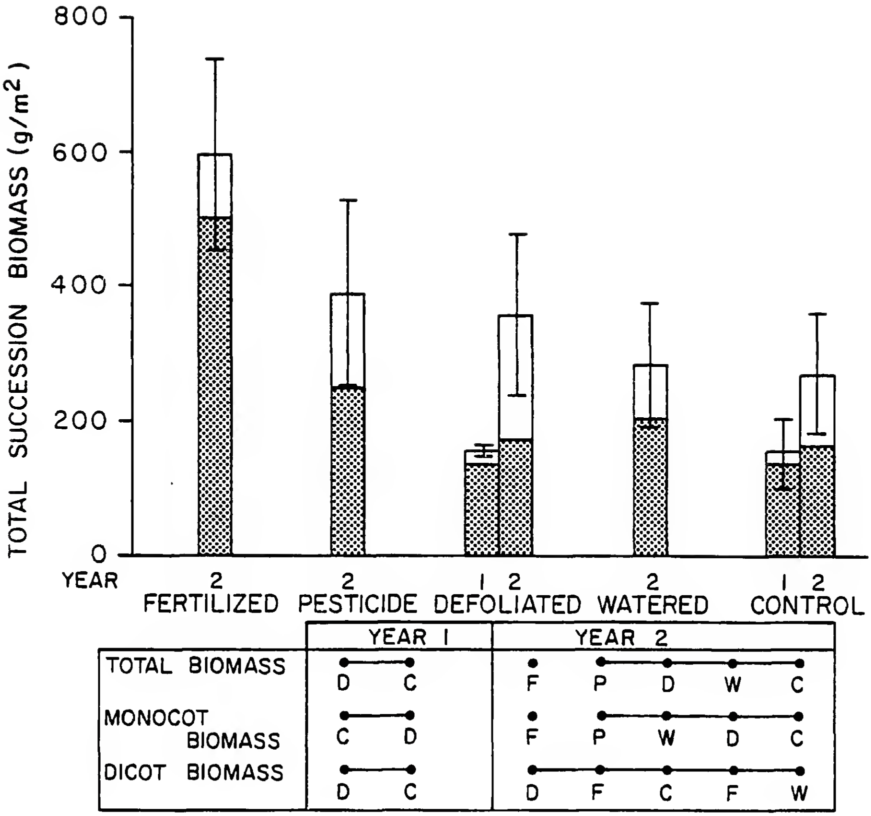

Figure 55. Successional monocot, dicot, and total aboveground biomass in the stress treatments, Years 1 and 2. Stippled portion of bar is monocot biomass, unstippled is dicot biomass, and s is shown for the total. Duncan's tests for treatment differences in monocot, dicot, and total biomass are shown in the box below the histogram. Treatments not connected by a common line are significantly different. C = control treatment, F = fertilized, P = pesticide, D = defoliated, W = watered.

either the total biomass of the successional vegetation or its monocot/dicot composition.

Aboveground biomass at flowering

Aboveground biomass at flowering of maize, sorghum, and cowpea was consistently, but nonsignificantly, greater in the four-crop system than in monoculture (except in fertilized cowpeas, where this measure was higher in monoculture) (Table 16). Pumpkin biomass at flowering, in contrast, was significantly higher in monoculture than in the four-crop system. Fertilization consistently increased biomass at flowering of all species (including successional monocots and dicots), but the difference from controls was significant only for maize, sorghum, and successional monocots.

LAI

Each species' LAI, adjusted for planting density, was compared among crop systems and treatments (Figures 56 and 57). Significant differences were few in the first sample in both years, which are omitted from the figures, and in the second sample in Year 1. In both years maize LAI was significantly lower in maize monoculture than in all intercrop systems except maize-sorghum. Sorghum LAI was consistently lower in sorghum monoculture than in either the maize-sorghum or four-crop intercrop, but the differences were not significant. Cowpea LAI was higher in monoculture than in either the maize-cowpea or four-crop intercrop in Year 1, but in Year 2 it was higher in the four-crop system than in monoculture; none of the differences were significant. Pumpkin LAI was

Table 16. Aboveground biomass of each species at flowering, Year 2. Data are $\bar{x} \pm s$, in g/m^2. Biomass of the crop species is adjusted for planting density in the intercrop. Duncan's tests (performed on samples of the four-crop and monoculture systems, for crop species) showed significantly greater biomass in fertilized than control plots for successional monocots, maize, and sorghum. Duncan's tests on samples of the control and fertilized treatments combined showed significantly greater biomass in monoculture than in the four-crop system for pumpkin.

SPECIES	CONTROL		FERTILIZED	
SUCCESSIONAL MONOCOTS	138. ± 79.0		385.3 ± 89.0	
SUCCESSIONAL DICOTS	51.9 ± 35.9		92.6 ± 47.0	
	FOUR-CROP	MONOCULTURE	FOUR-CROP	MONOCULTURE
MAIZE	302.0 ± 142.0	181.6 ± 44.9	587.5 ± 138.1	490.3 ± 151.2
SORGHUM	288.0 ± 128.6	255.5 ± 156.1	534.1 ± 62.8	467.4 ± 84.2
COWPEA	26.1 ± 20.7	8.3 ± 6.4	46.1 ± 44.7	77.0 ± 78.7
PUMPKIN	1.0 ± .5	53.7 ± 80.3	14.2 ± 22.9	65.2 ± 57.7

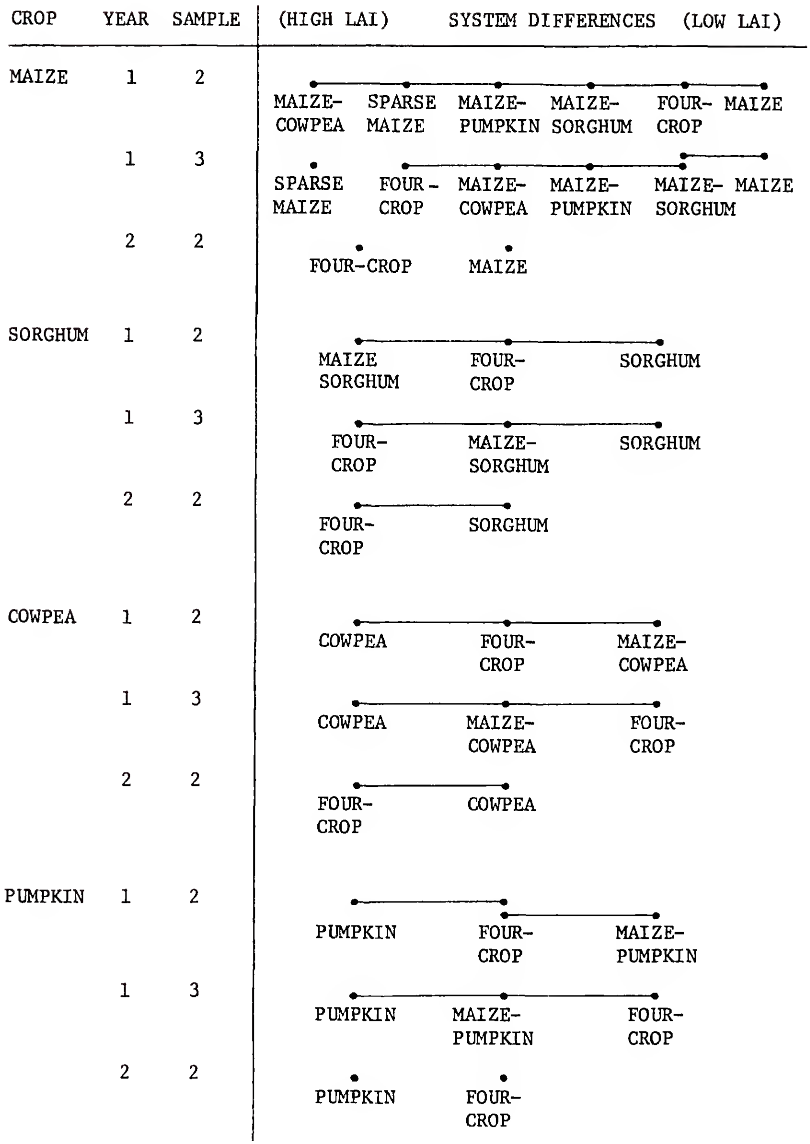

Figure 56. Maize, sorghum, cowpea, and pumpkin LAI differences among systems, Years 1 and 2. LAI in intercrop systems has been adjusted for planting density. Systems not sharing a common line are significantly different by Duncan's tests, performed on samples of all treatments combined in Year 2. Year 1 data were from the main control plots.

SPECIES	(HIGH LAI)	TREATMENT DIFFERENCES	(LOW LAI)
MAIZE	FERTILIZED	CONTROL	PESTICIDE
SORGHUM	FERTILIZED	PESTICIDE	CONTROL
COWPEA	PESTICIDE	FERTILIZED	CONTROL
PUMPKIN	FERTILIZED	CONTROL	PESTICIDE
SUCCESSIONAL MONOCOTS	FERTILIZED	PESTICIDE	CONTROL
SUCCESSIONAL DICOTS	FERTILIZED	CONTROL	PESTICIDE

Figure 57. Maize, sorghum, cowpea, pumpkin, successional monocot and successional dicot LAI differences among treatments, Year 2. LAI of crop species in intercrops has been adjusted for planting density. Treatments not sharing a common line are significantly different by Duncan's tests, performed on samples of both systems (four-crop and monoculture) combined for crop species.

consistently higher in the pumpkin monoculture than in either the maize-pumpkin or four-crop intercrop system.

Fertilization significantly increased LAI of maize, sorghum, cowpea, and successional monocots compared with the control treatment (Figure 57). Pumpkin and successional monocot LAI were also higher in fertilized plots than controls, but not significantly so. Pesticide spraying significantly increased cowpea LAI, but had no significant effect on the other species.

LAI at flowering

Maize and sorghum LAI at flowering, by the harvest method, were greater in intercrop than monoculture (significantly so for sorghum); LAI of cowpea was approximately equal in the simple and diverse systems, and pumpkin LAI was significantly greater in monoculture (Table 17). Fertilization increased the LAI of all agronomic species (significantly so for maize, sorghum, and cowpea). LAI at flowering was not calculated for successional monocots and dicots.

Leaf mass at defoliation

Maize defoliated leaf mass was higher in the maize-cowpea and sparse maize systems than in the maize monoculture, maize-sorghum, and maize-pumpkin systems in Year 1 (Figure 58). Sorghum defoliated leaf biomass did not vary significantly among systems. The mass of defoliated pumpkin leaves was higher in pumpkin monoculture than in the four-crop system in both years (a significant difference in Year 1 but not Year 2).

Table 17. LAI of each species by the harvest method at flowering, Year 2. Data are $\bar{x} \pm s$, and are adjusted for planting density in the intercrop system. Duncan's tests performed on samples of the four-crop and monoculture systems combined showed significantly greater LAI in fertilized than control plots for maize, sorghum, and cowpea. Duncan's tests on samples of the control and fertilized treatments combined showed significantly greater LAI in the four-crop system than in monoculture for sorghum, and significantly greater LAI in monoculture for pumpkin.

	CONTROL		FERTILIZED	
SPECIES	FOUR-CROP	MONOCULTURE	FOUR-CROP	MONOCULTURE
MAIZE	1.06 ± .47	.74 ± .17	1.82 ± .32	1.56 ± .43
SORGHUM	.99 ± .49	.54 ± .29	1.84 ± .28	1.06 ± .20
COWPEA	.31 ± .26	.09 ± .06	.48 ± .48	.74 ± .74
PUMPKIN	.01 ± .01	.71 ± 1.00	.35 ± .60	.80 ± .50

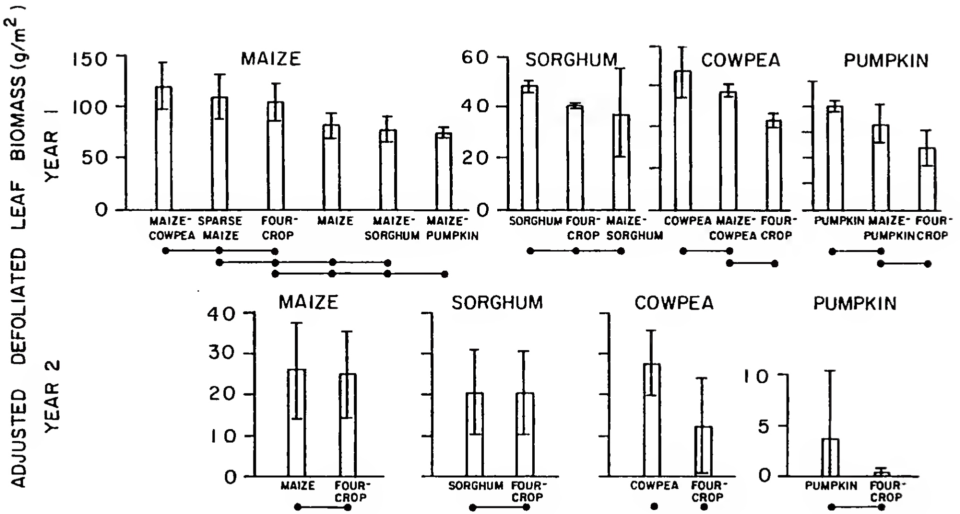

Figure 58. Defoliated leaf mass of each species, Years 1 and 2. Values were adjusted for planting density in intercrops. Systems not sharing a common line are significantly different by Duncan's tests.

Root biomass

Root biomass was not determined by-species in the Year 1 coring method. In Year 2 root biomass at flowering of maize and sorghum (0-15 cm depth) was higher in the four-crop intercrop than in monoculture (significantly so for maize); that of cowpea was approximately equal in the simple and diverse systems; and pumpkin rooting was significantly greater in monoculture than in the intercrop (Table 18). Rooting of all agronomic species was stimulated by fertilization (significantly so for maize, sorghum, and cowpea), but rooting of successional monocots and dicots was approximately equal in control and fertilized plots.

Roots were produced most abundantly by sorghum, maize, and successional monocots (16-24 g/m^2 in control plots); cowpea, pumpkin, and successional dicots produced many fewer roots (0-7 g/m^2 in control plots).

Survivorship and mortality

Control treatment. Maize and sorghum survivorship were generally high in both study years (less than 10 percent dying in the sampling period, Figures 59 and 60). Pumpkin survivorship was intermediate (less than 40 percent dead at the end of the sampling period, Figure 60), and cowpea survivorship was low in Year 1 and intermediate in Year 2 (Figure 60). Survivorship of each species generally did not vary significantly among systems. Pumpkin survivorship was, however, significantly higher in the monoculture than in the four-crop system in the first Year 2 sample. Also, cowpea survivorship was significantly higher in monoculture than in the four-crop system in several Year 2 samples.

Table 18. Root biomass of each species at flowering, Year 2. Data are $\bar{x} \pm s$ in g/m^2. Root biomass of crop species is adjusted for planting density in the intercrop. Duncan's tests (performed on samples of the four-crop and monoculture systems combined, for species) showed significantly greater biomass in fertilized than control plots for maize, sorghum, and cowpea. Duncan's tests on samples of the control and fertilized treatments combined showed significantly greater root biomass in the four-crop systems than in monoculture for maize, and significantly greater root biomass in monoculture for pumpkin.

SPECIES	CONTROL		FERTILIZED	
SUCCESSIONAL MONOCOTS	20.7 ± 17.0		15.7 ± 6.1	
SUCCESSIONAL DICOTS	6.9 ± 5.1		4.5 ± 2.6	
	FOUR-CROP	MONOCULTURE	FOUR-CROP	MONOCULTURE
MAIZE	16.2 ± 6.8	9.8 ± 1.2	51.6 ± 10.0	34.5 ± 10.5
SORGHUM	24.2 ± 10.4	23.9 ± 15.8	58.7 ± 12.1	47.6 ± 11.4
COWPEA	3.0 ± 2.1	2.0 ± .7	4.7 ± 3.3	7.6 ± 3.7
PUMPKIN	.2 ± .2	1.2 ± 1.6	.5 ± .7	1.6 ± 1.5

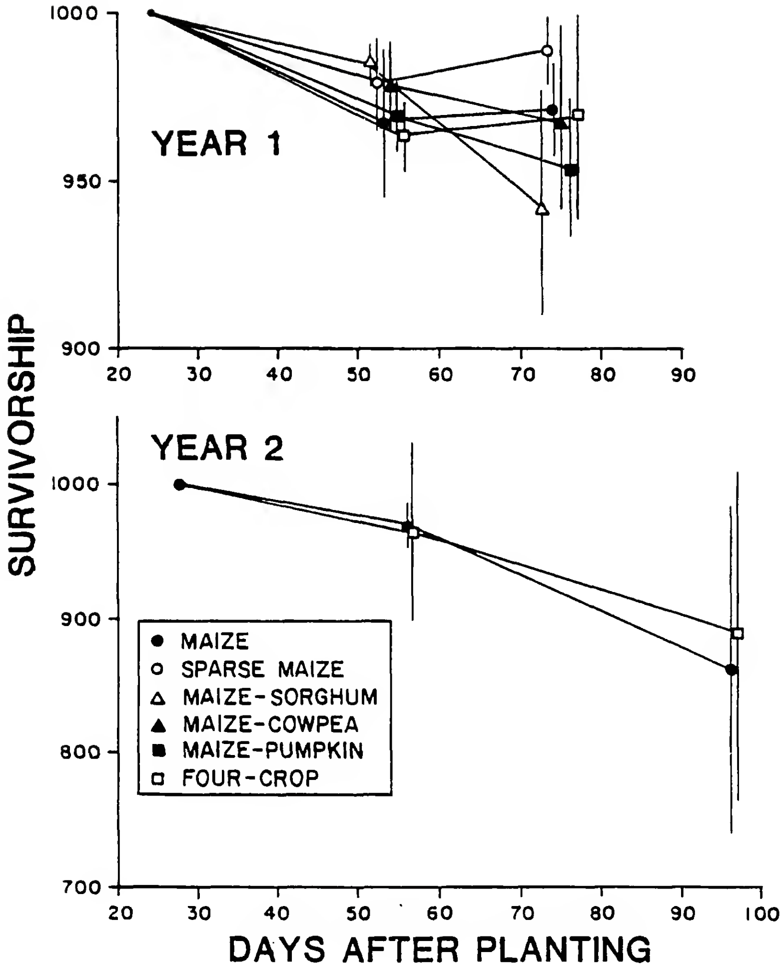

Figure 59. Maize survivorship in intercrops and monocultures in the control treatment, Years 1 and 2. Initial cohort was the established population at 24 and 28 days in Years 1 and 2, respectively. Duncan's tests, performed on samples of all treatments combined (not shown in the graph) gave no significant differences among systems.

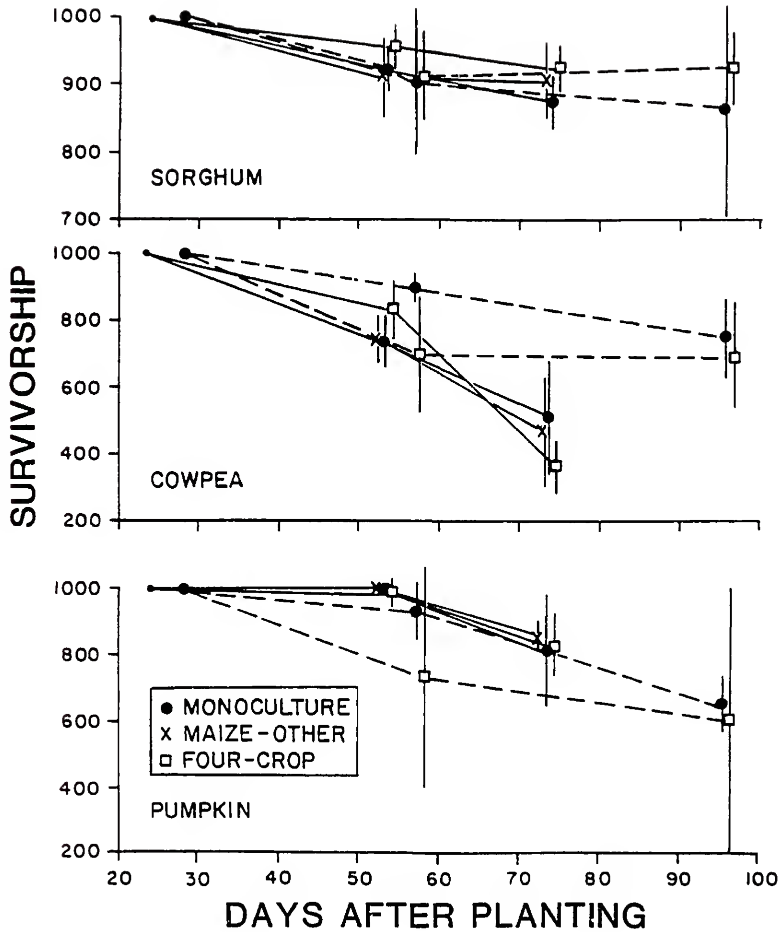

Figure 60. Sorghum, cowpea, and pumpkin survivorship in intercrops and monocultures in the control treatment, Years 1 and 2. Solid lines are Year 1; dashed lines are Year 2. Initial cohort was the established population at 24 and 28 days in Years 1 and 2, respectively. Duncan's tests in Year 2 cowpea were performed separately for each treatment; sorghum and pumpkin tests were performed on samples of all treatments combined. Significance of test results are given in the text.

Mortality rates of each crop species, calculated over the entire sampling period, did not vary significantly among systems (Figure 61), but sorghum mortality tended to be higher in monoculture than in the four-crop and maize-sorghum systems in both years. Cowpea mortality tended to be higher in the four-crop system than in the cowpea monoculture in both years.

Stress treatments. None of the Year 2 stress treatments had a significant effect on maize, sorghum, or pumpkin survivorship in either sample 2 or 3 (Figures 62, 63, and 65). Tests for treatment effects on cowpea survivorship were performed by-system because of significant system-by-treatment interaction (Figure 64). In both samples cowpea survivorship was significantly lower in the fertilization and control treatments than in the watering, pesticide, and defoliation treatments. In the cowpea monoculture, survivorship was again lowest in the control and fertilized plots, but the only significant treatment effect was higher survivorship in the pesticide-sprayed plots than in controls in sample 3.

Mortality rates of the crop species did not vary significantly from system to system in a combined sample of all stress treatments (Figure 66). Sorghum mortality tended to be higher in monoculture than in the four-crop system under all treatments; cowpea mortality tended to be higher in intercrop in the two highest-yielding treatments (control and fertilized); and pumpkin mortality tended to be higher in intercrop in all treatments except fertilization, where it was about equal to that in pumpkin monoculture. Maize mortality was higher in the intercrop than in monoculture in the defoliation and watering treatments.

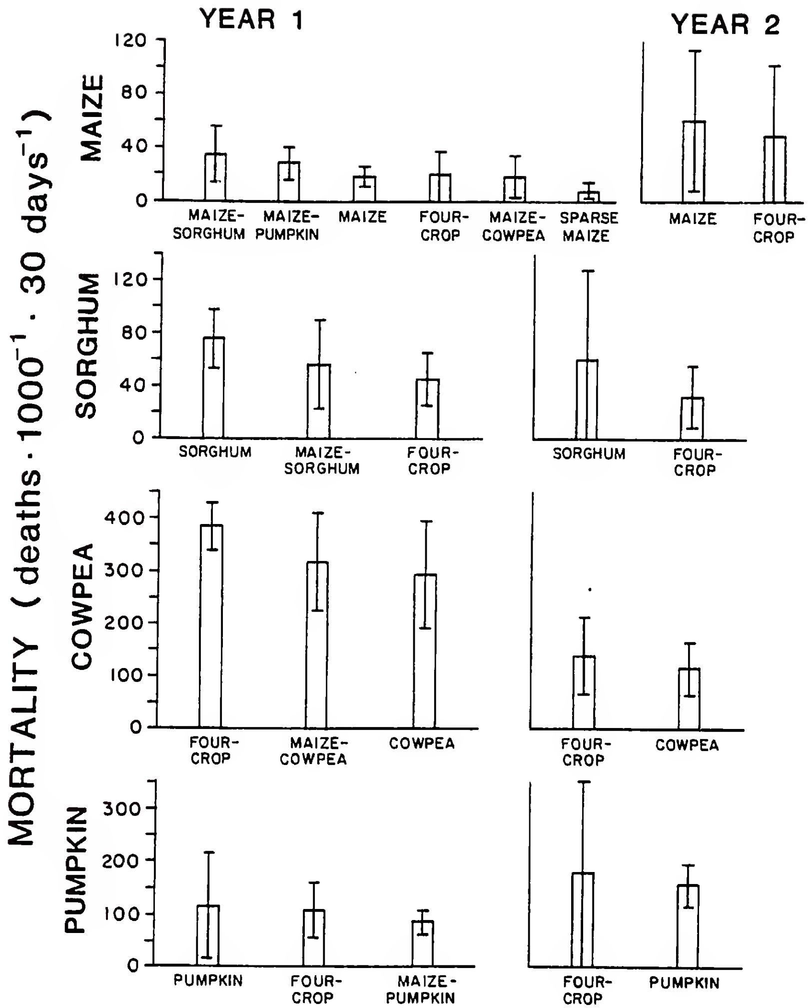

Figure 61. Mortality rate of each species in the control treatment, Years 1 and 2. Sampling period was day 24-74 in Year 1 and day 28-96 in Year 2. Duncan's tests, performed on samples of all treatments combined (not shown in the graph) gave no significant differences among systems.

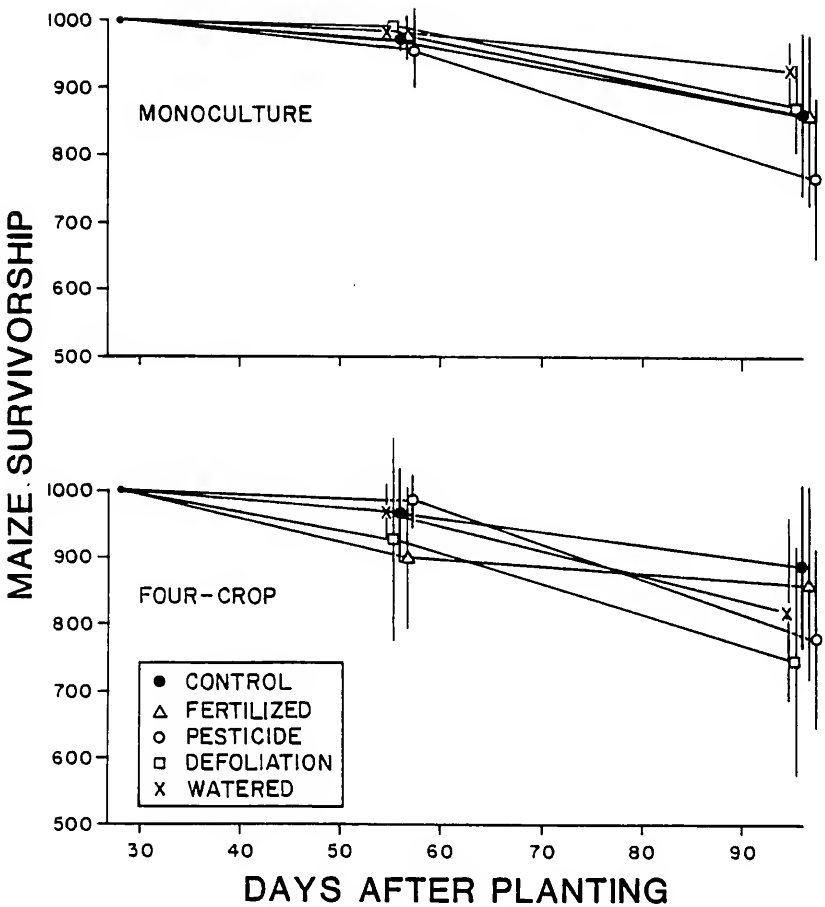

Figure 62. Maize survivorship in five treatments, Year 2. Initial cohort was the established population at day 28. Duncan's tests performed on a sample of both systems combined gave no significant differences among treatments.

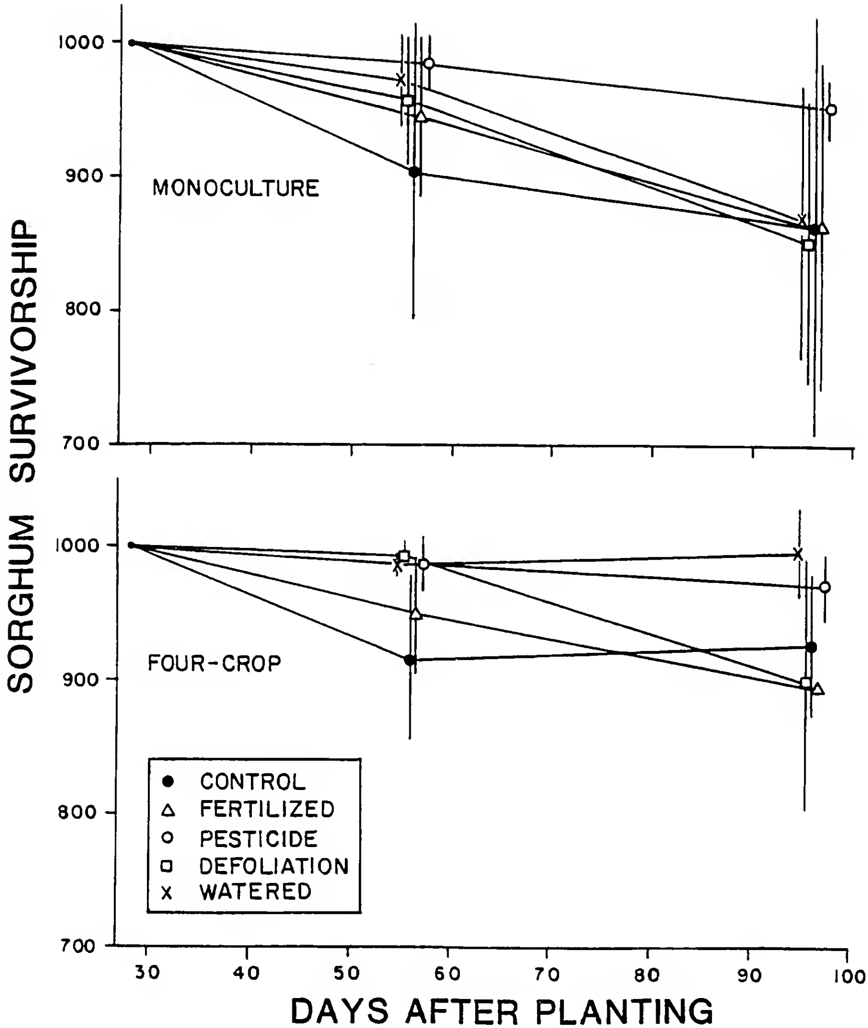

Figure 63. Sorghum survivorship in five treatments, Year 2. Initial cohort was the established population at day 28. Duncan's test performed on a sample of both systems combined gave no significant differences among treatments.

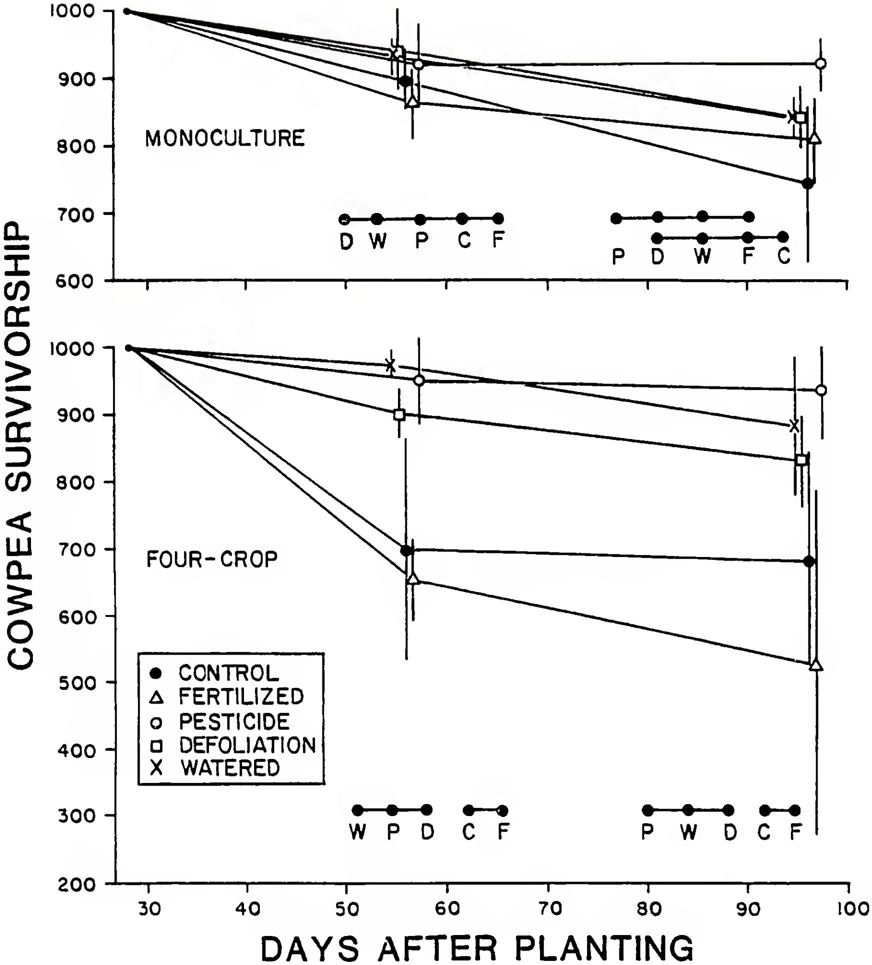

Figure 64. Cowpea survivorship in five treatments, Year 2. Initial cohort was the established population at day 28. Duncan's tests were performed separately for each system; results are shown below the corresponding samples. Treatments not connected by a common line are significantly different. C = control treatment; F = fertilized; P = pesticide; D = defoliated; W = watered.

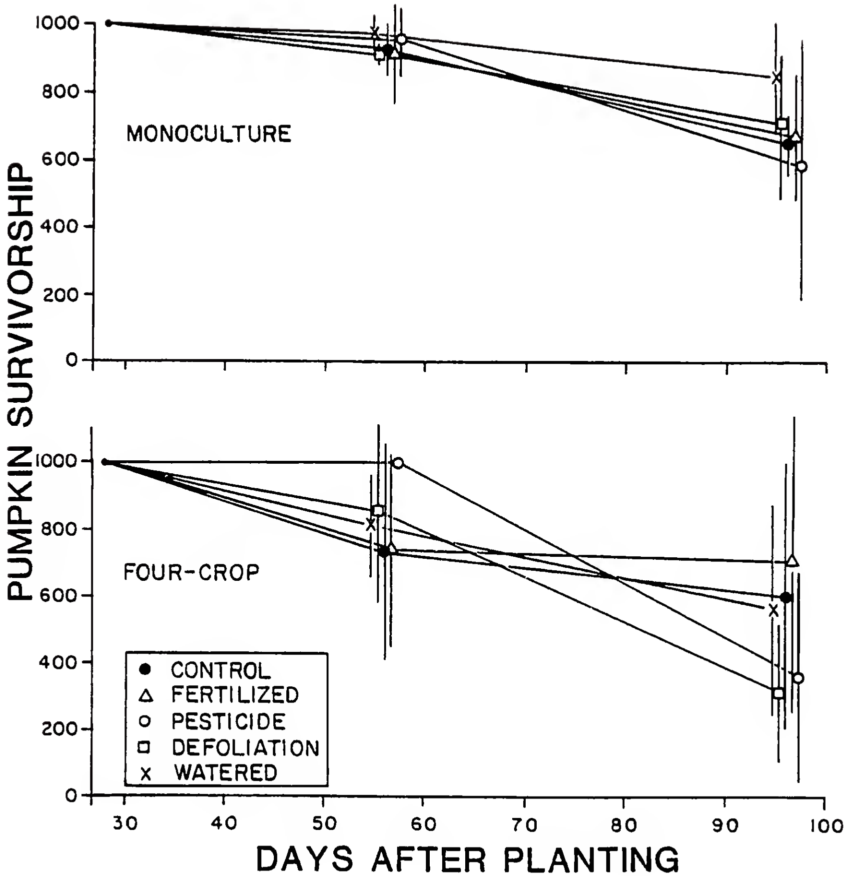

Figure 65. Pumpkin survivorship in five treatments, Year 2. Initial cohort was the established population at day 28. Duncan's tests performed on a sample of both systems combined gave no significant differences among treatments.

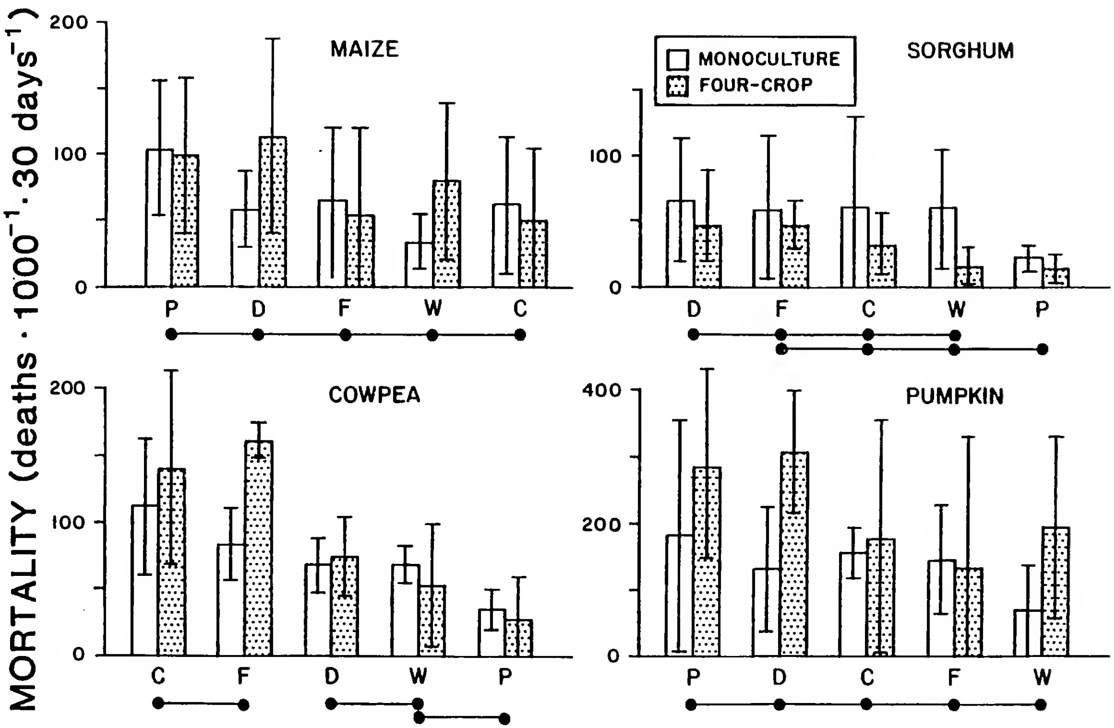

Figure 66. Mortality rates of each species in five treatments, Year 2. C = control treatment, F = fertilized; P = pesticide, D = defoliated, W = watered. The sampling period was 28-96 days. Treatments not connected by a common line are significantly different by Duncan's tests, performed on samples of the four-crop and monoculture systems combined.

Maize and pumpking mortality were highest in the pesticide and defoliation treatments, but no treatment effects were significant for those species. Sorghum mortality was lowest in the pesticide treatment and highest in the defoliation treatment (a significant difference, although neither differed significantly from the control). Cowpea mortality was significantly higher in the control and fertilized treatments than in the other treatments and significantly lower in the pesticide treatment than in any other treatment.

Stem length

All four crop species had typical logistic growth patterns in terms of stem length, with greatest stem elongation in the second sampling interval (Figures 66-71). Maximum growth occurred earlier and stopped sooner in sorghum than in maize. Cowpea stem elongation was steady throughout the growing season, with highest growth rates in the second interval. Pumpkin grew slowly during the first interval, but continued to elongate, at a rate of about 4 cm/day, late in the growing season.

Maize stem length was consistently greater in the sparse maize, maize-pumpkin, and maize-cowpea systems than in the four-crop, maize-sorghum, and maize monoculture systems in Year 1 (Figures 67 and 68). In Year 2, maize was very slightly (nonsignificantly) taller in the four-crop system than in maize monoculture in both samples.

Sorghum height increased more slowly during the middle of the growing season in Year 2 than in Year 1 (Figure 69). Sorghum was slightly taller in monoculture than in the four-crop system in the first two samples in both years. Sorghum grew rapidly in the intercrop

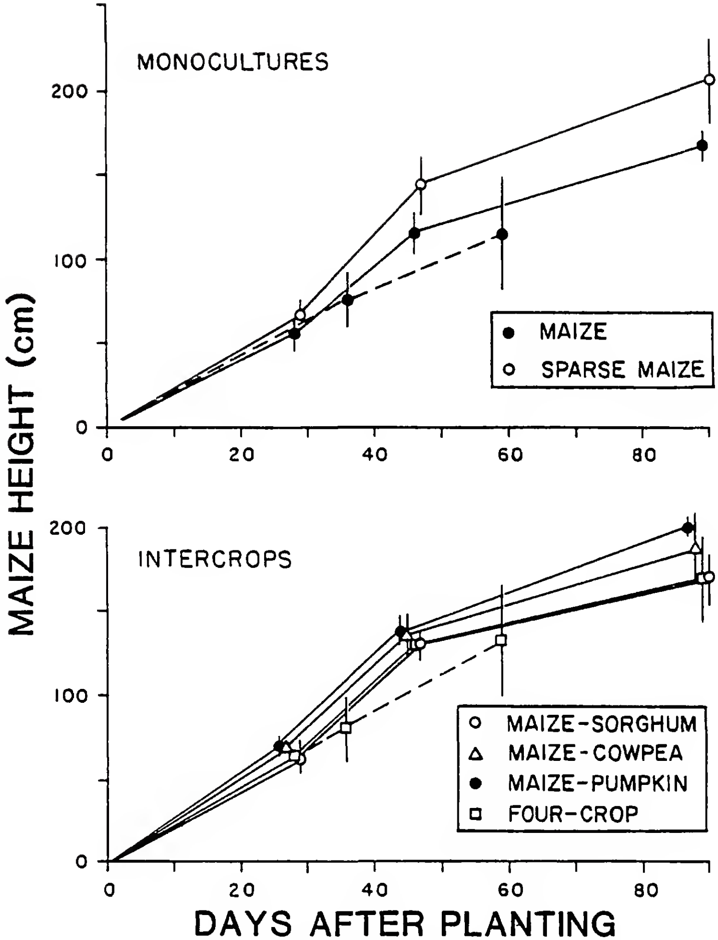

Figure 67. Maize height by time in the control treatment, Years 1 and 2. Solid lines are Year 1; dashed lines are Year 2. Significance of system differences by Duncan's tests (performed on samples of all treatments combined) is shown in Figure 68.

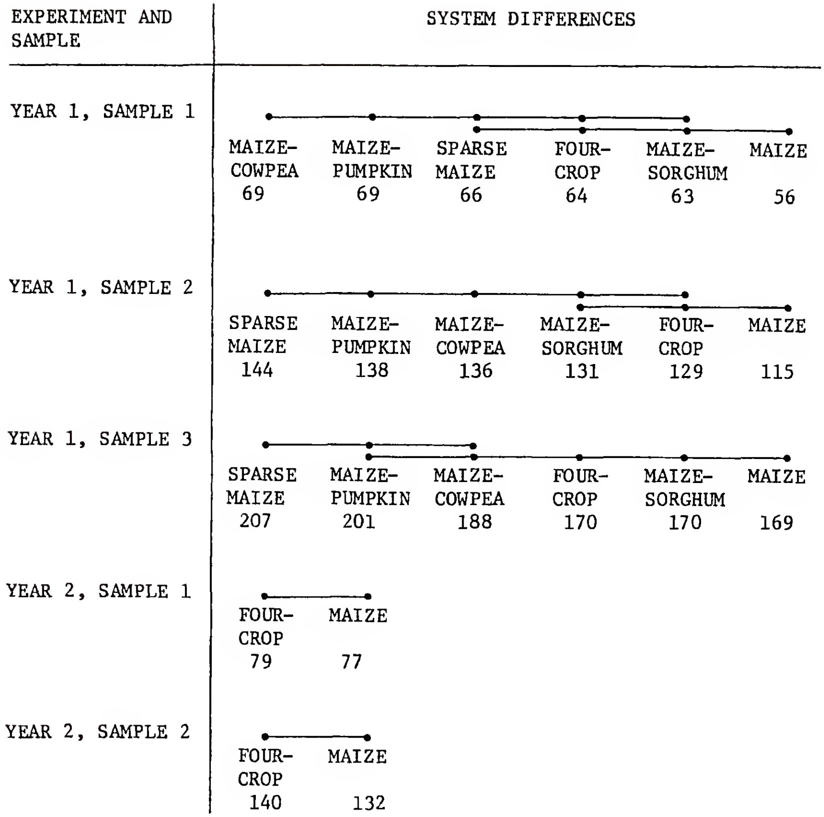

Figure 68. Maize height differences among systems, Years 1 and 2. Year 1 means (cm) are from the main control plots; Year 2 means are all treatments combined. Systems not sharing a common line are significantly different by Duncan's tests, performed on samples of all treatments combined in Year 2.

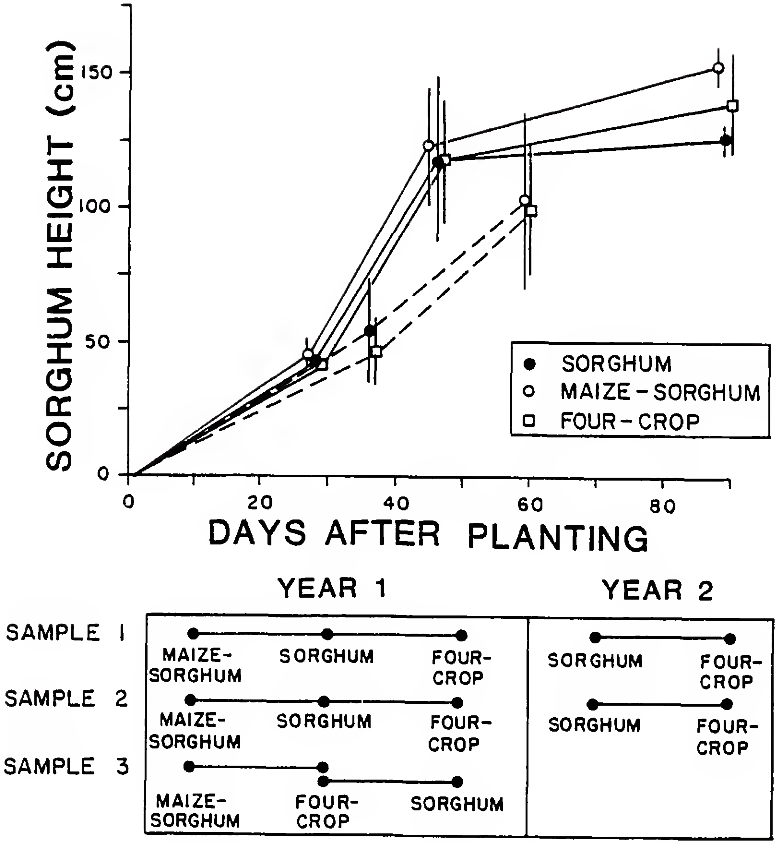

Figure 69. Sorghum height by time in the control treatment, Years 1 and 2. Solid lines are Year 1; dashed lines are Year 2. Systems not connected by a common line are significantly different by Duncan's tests, performed on samples of all treatments combined in Year 2.

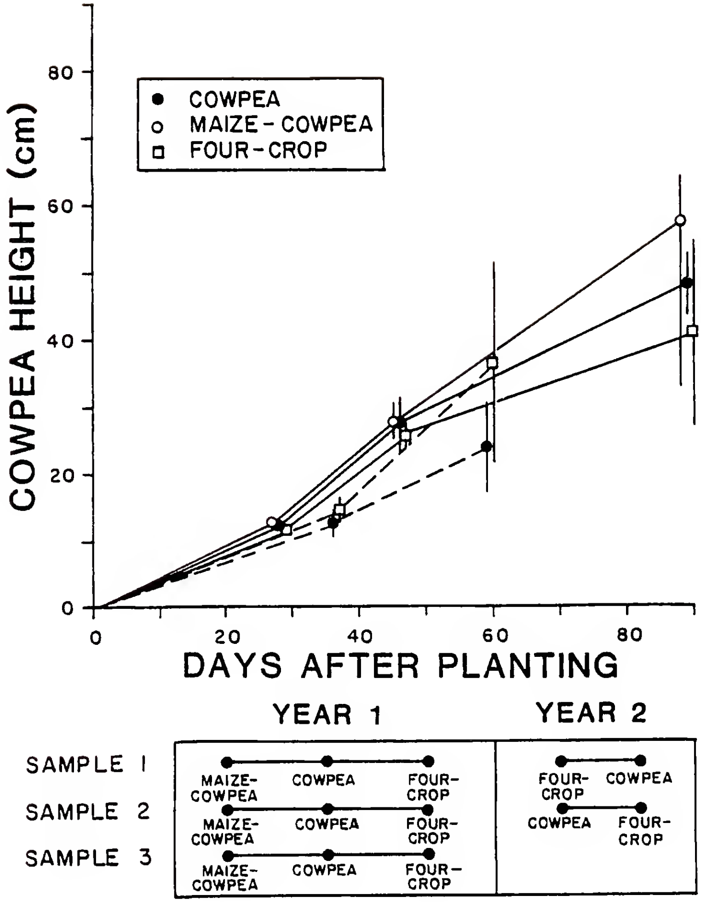

Figure 70. Cowpea height by time in the control treatment, Years 1 and 2. Solid lines are Year 1; dashed lines are Year 2. Systems not connected by a common line are significantly different by Duncan's tests, performed on samples of all treatments combined in Year 2.

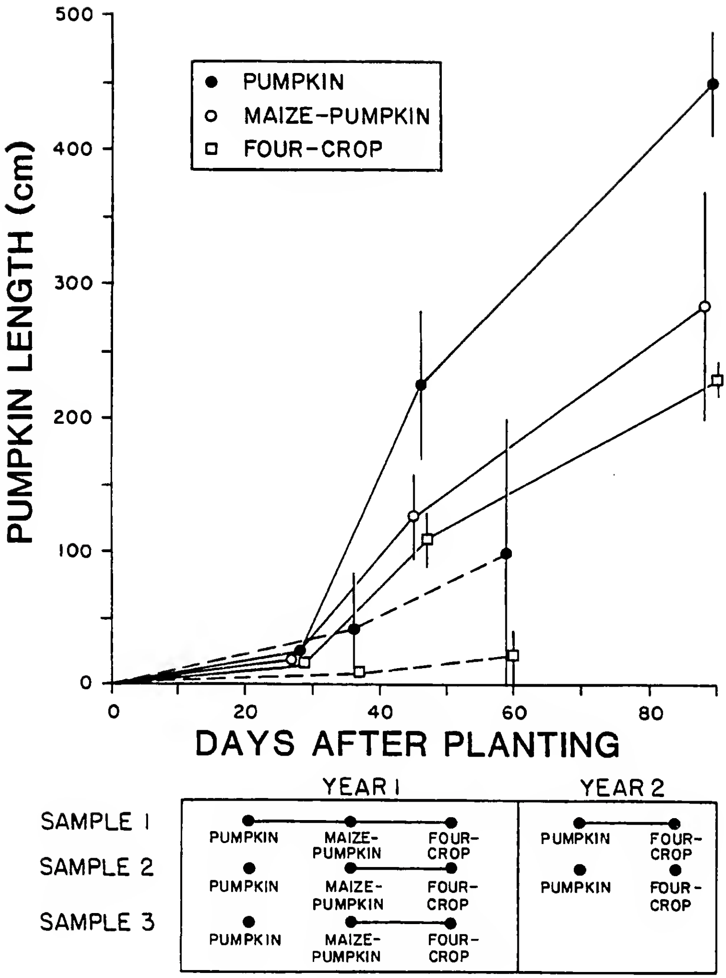

Figure 71. Pumpkin length by time in the control plots, Years 1 and 2. Solid lines are Year 1; dashed lines are Year 2. Systems not connected by a common line are significantly different by Duncan's tests, performed on samples of all treatments combined in Year 2.

SPECIES	TREATMENT DIFFERENCES				
MAIZE	FERTILIZED 197	DEFOLIATED 132	CONTROL 124	WATERED 113	PESTICIDE 110
SORGHUM	FERTILIZED 131	PESTICIDE 110	CONTROL 101	DEFOLIATED 101	WATERED 91
COWPEA	PESTICIDE 67	FERTILIZED 56	DEFOLIATED 42	WATERED 37	CONTROL 30
PUMPKIN	FERTILIZED 122	DEFOLIATED 68	CONTROL 64	WATERED 34	PESTICIDE 18

Figure 72. Maize, sorghum, cowpea and pumpkin length differences among treatments, Year 2. Means (cm) are from sample 2, and include both systems (four-crop and monoculture). Treatments not sharing a common line are significantly different by Duncan's tests, performed on samples of both systems combined.

systems at the end of the growing season, however, and was significantly taller in the maize-sorghum system than in sorghum monoculture in the third length sample (taken in Year 1 only).

Differences in cowpea stem length among systems (Figure 70) were not significant in any of the Year 1 and 2 samples.

Pumpkin stem length (Figure 71) was significantly greater in monoculture than in the maize-pumpkin and four-crop systems in all samples except the first length sample in both years.

The Year 2 stress treatments had some significant effects on maize, sorghum, cowpea, and pumpkin growth (Figure 72). Fertilization significantly increased maize and sorghum height compared with all other treatments, significantly increased cowpea length compared with the control, and significantly increased pumpkin length over that of all other treatments except defoliation. Cowpea length was greatest in the pesticide treatment (significantly more than all other treatments except fertilization). Other treatment effects on stem length were not significant, but maize and pumpkin stem length were both lowest in the pesticide-treated plots, while sorghum stem length was second highest in the sprayed plots (almost 20 cm taller than controls). Defoliated plants of all four species had approximately the same stem length as controls. The effect of defoliation was greatest in cowpea, where mean stem length in defoliated plots was 12 cm greater than in controls.

Measures of Biomass Distribution

Allocation ratios

The ratio of maize edible to total aboveground biomass (allocation ratio) was significantly higher in the four-crop system than in

monoculture in both years 1 and 2 (Figure 73). In Year 1 the ratio was highest in the four-crop and maize-cowpea systems and lowest in the maize-sorghum and maize systems. The defoliation treatment significantly increased the allocation ratio in Year 1 but not in Year 2. In Year 2, pesticide spraying significantly reduced the allocation ratio, but allocation ratios in the fertilized and watered treatments were not significantly different from controls.

Sorghum allocation ratio (Figure 74) was significantly higher in the sorghum monoculture than in either intercrop system in Year 1 small plots, but no significant system effects were found in the Year 1 main plots or Year 2 plots. The stress treatments had no significant effect on sorghum allocation ratio in either year, compared with controls.

Cowpea allocation ratio (Figure 75) was significantly higher in the maize-cowpea system than in cowpea monoculture and four-crop systems in the Year 1 main plots, but no significant differences were found in the other experiments. The stress treatments did not cause any significant changes in allocation ratio compared with controls.

Pumpkin allocation ratio (Figure 76) was significantly higher in monoculture than in the four-crop system in Year 2, and pumpkin edible yield was zero in Year 1. None of the Year 2 stress treatments caused significant change in allocation ratio from that of controls.

Root/shoot ratios

Root/shoot ratios were higher in the two dicot species (cowpea and pumpkin) than in the more productive monocot species, maize and sorghum (Table 19). Cowpea and pumpkin root/shoot ratios were higher in the

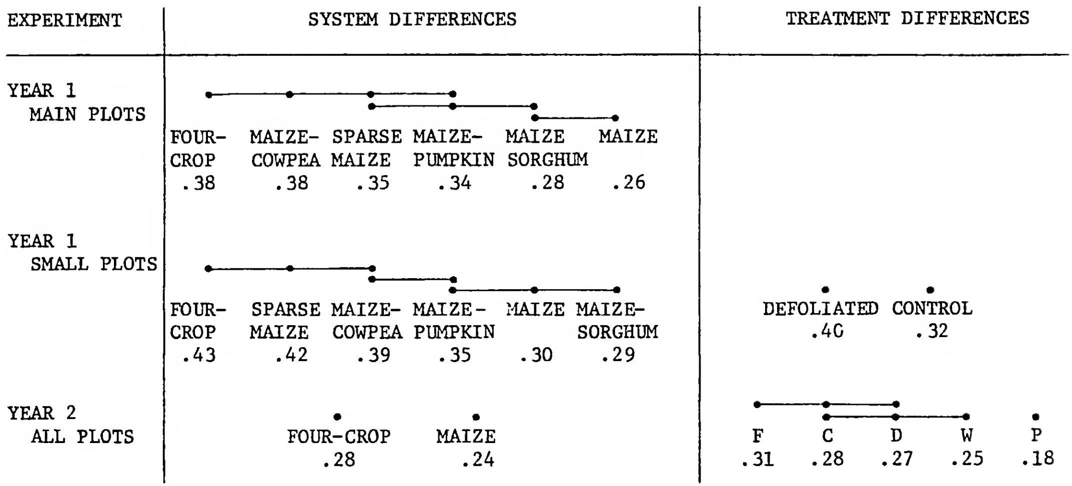

Figure 73. Maize allocation ratio, Years 1 and 2. Systems or treatments not sharing a common line are significantly different by Duncan's tests, performed on samples of all systems or treatments combined. C=control treatment; F=fertilized, P=pesticide; D=defoliated; W=watered.

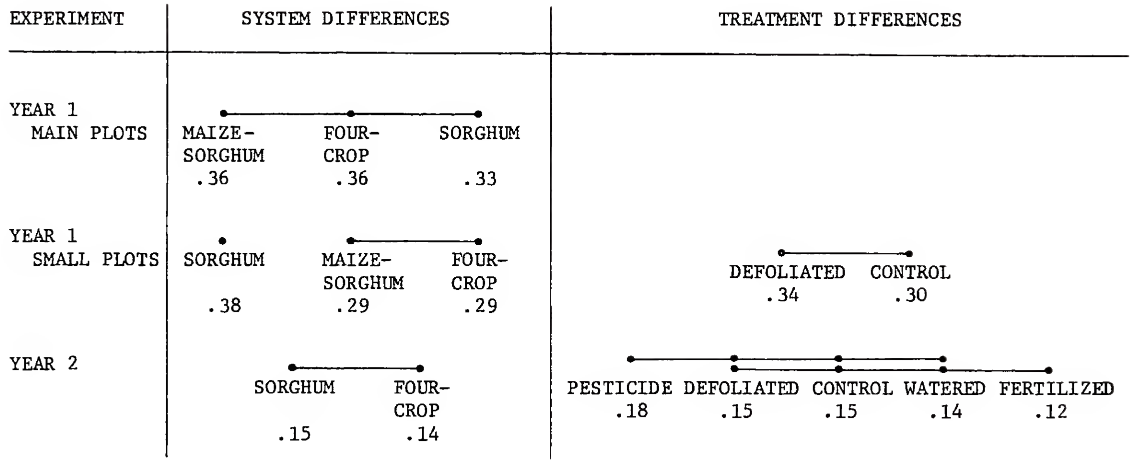

Figure 74. Sorghum allocation ratio, Years 1 and 2. Systems or treatments not sharing a common line are significantly different by Duncan's tests, performed on samples of all systems or treatments combined.

EXPERIMENT	SYSTEM DIFFERENCES			TREATMENT DIFFERENCES				
YEAR 1 MAIN PLOTS	MAIZE-COWPEA .11	COWPEA .07	FOUR-CROP .06					
YEAR 1 SMALL PLOTS	COWPEA .18	MAIZE-COWPEA .12	FOUR-CROP .11			CONTROL .15	DEFOLIATED .12	
YEAR 2	FOUR-CROP .12	COWPEA .09		PESTICIDE .17	WATERED .12	CONTROL .10	DEFOLIATED .08	FERTILIZED .06

Figure 75. Cowpea allocation ratio, Years 1 and 2. Systems or treatments not sharing a common line are significantly different by Duncan's tests, performed on samples of all systems or treatments combined.

SYSTEM DIFFERENCES		TREATMENT DIFFERENCES				
PUMPKIN	FOUR-CROP	DEFOLIATED	FERTILIZED	CONTROL	PESTICIDE	WATERED
.32	0	.28	.26	.15	.09	.07

Figure 76. Pumpkin allocation ratio, Year 2. Allocation ratio was zero in all plots in Year 1. Systems or treatments not sharing a common line are significantly different by Duncan's tests, performed on samples of all systems or treatments combined.

Table 19. Root/shoot ratio of each species at flowering, Year 2. Data are $\bar{x} \pm s$. Duncan's tests (performed on samples of the four-crop and monoculture systems combined, for crop species) showed significantly greater root/shoot ratios in fertilized than control plots for maize, and significantly greater root/shoot ratios in control than fertilized plots for successional monocots, successional dicots, and pumpkin. Duncan's tests on samples of the control and fertilized treatments combined showed significantly greater root/shoot ratios in intercrop than monoculture for pumpkin, and greater root/shoot ratios in monoculture for cowpea.

	CONTROL		FERTILIZED	
SUCCESSIONAL MONOCOTS	.134 ± .047		.040 ± .006	
SUCCESSIONAL DICOTS	.127 ± .017		.055 ± .018	
	FOUR-CROP	MONOCULTURE	FOUR-CROP	MONOCULTURE
MAIZE	.057 ± .012	.056 ± .014	.089 ± .013	.072 ± .013
SORGHUM	.088 ± .029	.092 ± .017	.110 ± .021	.101 ± .008
COWPEA	.146 ± .101	.315 ± .123	.120 ± .039	.199 ± .128
PUMPKIN	.245 ± .160	.714 ± .999	.034 ± .003	.801 ± .505

four-crop system than in monoculture (significantly so for pumpkin); the root/shoot ratios of maize and sorghum were approximately the same in intercrop and monoculture.

Fertilization reduced the root/shoot ratio of successional monocots, successional dicots, pumpkin, and cowpea (significantly so for all but cowpea), but increased the root/shoot ratio for maize and sorghum (significantly so for maize).

Specific leaf mass

Sorghum leaves weighed significantly more per unit leaf area in monoculture than in the four-crop system; the same trend was found for maize, cowpea, and pumpkin leaves (Table 20). Leaves of all agronomic species except maize tended to weigh less per unit leaf area in the fertilized than in the control treatment; the difference was statistically significant for pumpkin. Specific leaf mass of successional monocots was lower than that of the agronomic monocots maize and sorghum. Specific leaf mass of successional dicot leaves was approximately equal to that of cowpea leaves (under all systems and treatments). Pumpkin leaves were the lightest per unit area of all types sampled.

Miscellaneous yield parameters

Maize yield parameters. Maize cob production and yield per cob varied from system to system in the same patterns as did maize edible and total yield (Figure 77). Cob production and yield per cob were highest in the maize and maize-cowpea systems and lowest in the maize-sorghum and maize monoculture systems. Cob production and edible yield per cob were slightly, but nonsignificantly, higher in defoliated than

Table 20. Specific leaf mass of each species at flowering, Year 2. Data are $\bar{x} \pm s$ in g/m^2 leaf. Duncan's tests (performed on samples of the four-crop and monoculture systems combined, for crop species) showed significantly greater specific leaf mass in control than fertilized plots for pumpkin. Duncan's tests performed on samples of the control and fertilized treatments combined showed significantly greater specific leaf mass in monoculture than in the four-crop intercrop for sorghum.

	CONTROL		FERTILIZED	
SUCCESSIONAL MONOCOTS	56.98 ± 8.76		60.36 ± 17.65	
SUCCESSIONAL DICOTS	52.58 ± 8.29		50.16 ± 13.82	
	FOUR-CROP	MONOCULTURE	FOUR-CROP	MONOCULTURE
MAIZE	88.07 ± 43.81	89.38 ± 42.18	79.34 ± 8.97	94.05 ± 42.34
SORGHUM	72.92 ± 7.49	115.95 ± 14.72	73.22 ± 17.18	99.28 ± 16.49
COWPEA	55.37 ± 14.46	63.62 ± 13.74	53.86 ± 7.11	54.90 ± 8.73
PUMPKIN	34.63 ± 2.50	52.20 ± 13.82	26.84 ± 4.42	34.63 ± 2.50

PARAMETER	SYSTEM DIFFERENCES					
COB PRODUCTION (cobs/m^2)	SPARSE MAIZE	MAIZE-COWPEA	FOUR-CROP	MAIZE-PUMPKIN	MAIZE-SORGHUM	MAIZE
	3.61	3.47	3.45	2.88	2.77	2.31
YIELD/COB (g edible yield/cob)	MAIZE-COWPEA	SPARSE MAIZE	MAIZE-PUMPKIN	FOUR-CROP	MAIZE-SORGHUM	MAIZE
	63.29	62.28	52.86	52.58	35.29	28.66

Figure 77. Maize cob production and edible yield/cob, Year 1. Cob production data were adjusted for planting density in the intercrop systems. Data are from the main control plots. Systems not sharing a common line are significantly different by Duncan's tests.

control plots (mean cob production = 2.65 and 2.55, respectively; mean yield per cob = 47.13 and 42.54 g, respectively).

Sorghum yield parameters. Sorghum head production (Figure 78) was significantly higher in the four-crop intercrop than in sorghum monoculture. The pesticide and defoliation treatments significantly reduced head production compared with the control and fertilization treatments. Edible yield per head (Figure 78) was not significantly different in the four-crop and sorghum monoculture systems; pesticide spraying, however, increased yield per head to a level significantly higher than that of the control, defoliation, and watering treatments. Fullness of heads (percent heads with more than 75 percent of seeds filled) was also approximately the same in the intercrop and monoculture systems. The stress treatments had no significant effect on head filling, but head filling was highest in the watering treatment (32 percent) and lowest in the fertilization and defoliation treatments (21 and 25 percent, respectively). Sorghum tillering (Figure 79) was higher in the four-crop system than in sorghum monoculture in both years, but the difference was significant only in Year 2. Tillering was highest in the fertilized treatment (61.6 percent, significantly higher than all other treatments). Pesticide spraying reduced tillering to a level significantly lower than that of the fertilized, control, and watered treatments.

Cowpea yield parameters. In Year 1, number of cowpea pods/plant, number of edible seeds/pod, and percent edible seeds (by number) did not vary significantly from system to system (Figure 80). All three variables were, however, highest in the cowpea monoculture and lowest

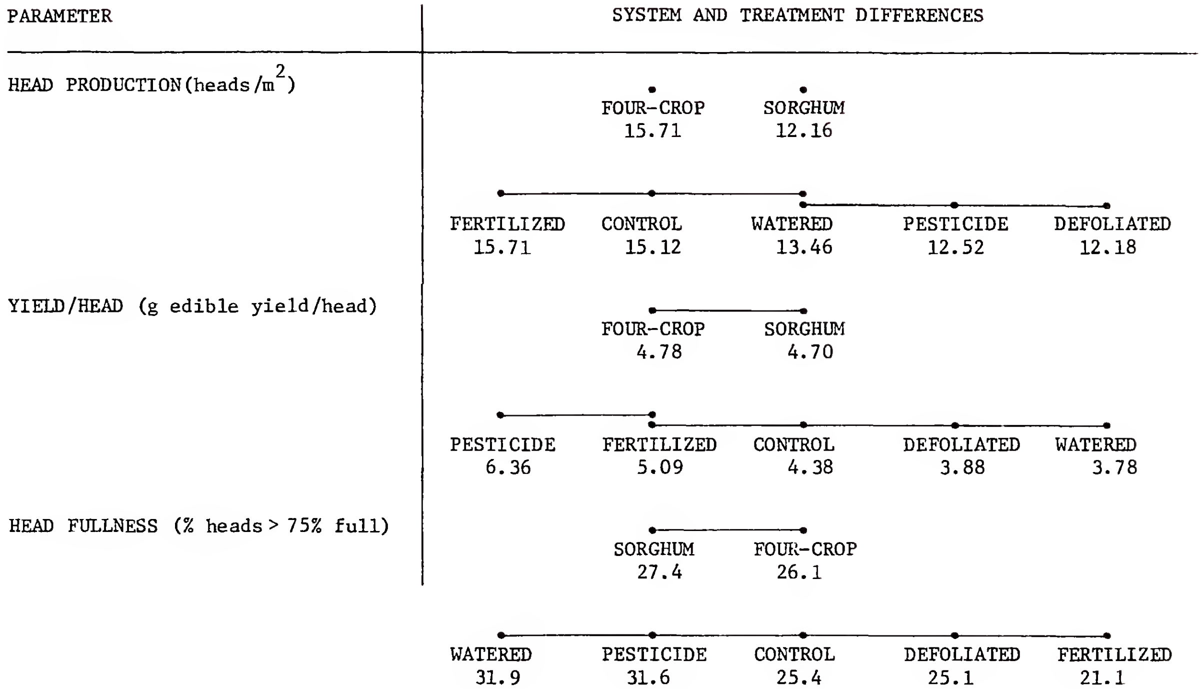

Figure 78. Sorghum head production, edible yield/head, and fullness of heads, Year 2. System means include all treatments; treatment means include all systems. Head production data were adjusted for planting density in the intercrop systems. Systems or treatments not sharing a common line are significantly different by Duncan's tests, performed on samples of all systems or treatments combined.

EXPERIMENT	SYSTEM AND TREATMENT DIFFERENCES				
YEAR 1 MAIN PLOTS	FOUR-CROP 56.0	SORGHUM 52.7	MAIZE-SORGHUM 52.7		
YEAR 2	FOUR-CROP 52.6	SORGHUM 36.9			
	FERTILIZED 61.6	CONTROL 47.4	WATERED 41.5	DEFOLIATED 39.4	PESTICIDE 31.3

Figure 79. Sorghum tillering, Years 1 and 2. Data are percent plants with one or more tillers, and are from the main control plots in Year 1, all plots in Year 2. In Year 2, system means include all treatments, treatment means include all systems, and Duncan's tests were performed on a sample of all systems or treatments combined.

PARAMETER	SYSTEM DIFFERENCES		
PODS/PLANT	COWPEA 4.21	MAIZE-COWPEA 4.01	FOUR-CROP 2.26
TOTAL NUMBER OF SEEDS/POD	MAIZE-COWPEA 13.02	COWPEA 12.98	FOUR-CROP 12.29
NUMBER OF EDIBLE SEEDS/POD	COWPEA 5.53	MAIZE-COWPEA 4.43	FOUR-CROP 3.48
PERCENT EDIBLE SEEDS (by number)	COWPEA 41.5	MAIZE-COWPEA 33.8	FOUR-CROP 28.5
PERCENT EDIBLE SEEDS (by mass)	MAIZE-COWPEA 83.2	COWPEA 72.4	FOUR-CROP 71.3

Figure 80. Cowpea yield parameters, Year 1. Data are from the main control plots. Systems not sharing a common line are significantly different by Duncan's tests.

PARAMETER	SYSTEM AND TREATMENT DIFFERENCES				
PERCENT EDIBLE SEEDS (by number)		FOUR-CROP 53.6		COWPEA 42.6	
	WATERED 58.7	PESTICIDE 57.4	CONTROL 48.3	DEFOLIATED 41.7	FERTILIZED 35.3
PERCENT EDIBLE SEEDS (by mass)		FOUR-CROP 50.7		COWPEA 49.4	
	PESTICIDE 54.0	CONTROL 53.5	WATERED 48.5	DEFOLIATED 48.1	FERTILIZED 44.7

Figure 81. Cowpea percent edible seeds (by number and mass), Year 2. System means include all treatments, and treatment means include both systems (four-crop and monoculture). Systems or treatments not sharing a common line are significantly different by Duncan's tests performed on samples of all systems or treatments combined despite slight system-by-treatment interaction (p=.043).

in the four-crop system (except seeds/pod, slightly higher in the maize-cowpea system than in cowpea monoculture). Percent edible seeds (by mass) was significantly higher in the maize-cowpea system than in the four-crop system in Year 1. In Year 2 (Figure 81), the four-crop system had slightly higher percent edible seeds (by both mass and number) than the cowpea monoculture, but the difference was not significant.

Defoliation had no significant effect on pods/plant, total seeds/pod, edible seeds/pod, or percent edible seeds (by mass or number) in Year 1. In Year 2 the stress treatments had no significant effect on percent edible seeds (by mass) compared with the control. Percent edible seeds (by number) was, however, significantly higher in the pesticide than in the fertilization treatment (Figure 81).

Cowpea third-leaf area did not vary significantly among systems in Year 1 (Figure 82). In Year 2, the four-crop system had significantly larger leaves than the cowpea monoculture in the control treatment, possibly due to unusually wet cowpea monoculture control plots early in the growing season. Cowpeas in the still-intact defoliation plots had large third-leaves, mean = 64.7 cm^2. In the fertilized and pesticide-sprayed plots, third-leaf area in the four-crop and cowpea monoculture systems was not significantly different. Pesticide spraying significantly increased third-leaf area in both the four-crop and cowpea monoculture systems compared with controls; fertilization had no significant effect.

Pumpkin yield parameters. Both pumpkin fruit production (number/m^2) and fruit mass (g/fruit) were significantly greater in the pumpkin monoculture than in the four-crop system (Figure 83). Pumpkin fruit setting (measured on day 80, Year 1) was also significantly higher in

TREATMENT OR SYSTEM	SYSTEM AND TREATMENT DIFFERENCES		
CONTROL (YEAR 1)	COWPEA 85.9	MAIZE-COWPEA 79.4	FOUR-CROP 71.0
CONTROL (YEAR 2)	FOUR-CROP 49.8	COWPEA 29.9	
FERTILIZED (YEAR 2)	FOUR CROP 46.8	COWPEA 45.9	
PESTICIDE (YEAR 2)	COWPEA 69.5	FOUR-CROP 68.5	
COWPEA (YEAR 2)	PESTICIDE 69.4	FERTILIZED 45.9	CONTROL 29.9
FOUR-CROP (Year 2)	PESTICIDE 68.5	CONTROL 49.8	FERTILIZED 47.8

Figure 82. Cowpea third-leaf area, Years 1 and 2. Systems or treatments not sharing a common line are significantly different by Duncan's tests, performed separately for each system and treatment. Defoliated and watered treatments are omitted because the sample was taken before those treatments were effective.

PARAMETER	SYSTEM AND TREATMENT DIFFERENCES				
PUMPKIN FRUIT PRODUCTION, YEAR 2 (no./m^2)	PUMPKIN .15	FOUR-CROP 0			
	FERTILIZED .17	DEFOLIATED .09	CONTROL .07	WATERED .03	PESTICIDE .01
PUMPKIN FRUIT SETTING, YEAR 1 (no./m^2)	PUMPKIN 1.34	FOUR-CROP .44	MAIZE-PUMPKIN .38		
PUMPKIN FRUIT MASS, YEAR 2 (g/fruit)	FERTILIZED 281.2	DEFOLIATED 214.7	CONTROL 137.7	WATERED 95.8	PESTICIDE 38.2

Figure 83. Pumpkin fruit production and fruit mass, Year 2, and fruit setting, Year 1. Fruit production and fruit setting data were adjusted for planting density in the intercrop systems. Systems or treatments not sharing a common line are significantly different. Fruit production system means include all treatments, treatment means include both systems (four-crop and monoculture), and Duncan's tests were performed on a sample of all systems or treatments combined. Fruit mass means include all treatments, but treatment means exclude the four-crop system, where pumpkin yield was zero in all plots. Year 1 fruit setting data are from the main control plots at day 80; no fruits matured to harvest in any system.

monoculture than in either the maize-pumpkin or four-crop intercrops, but none of the fruits matured to harvest. Fertilization increased both number and biomass of pumpkin fruits, and pesticide spraying decreased both, but neither treatment caused significant deviation from controls.

Correlations Among Direct Productivity Measures

Correlations among the direct measures of biomass accretion indicate the degree to which a particular measure reflects growth in general. Because of the dissimilar structure and growth processes of different species, the question of correlation among measures of biomass accretion was approached by-species (Tables 21-26) as well as across systems (presented earlier, Table 6). For each species, correlations among the variables were calculated for a complete sample of all plots (all systems and treatments) in which the species occurred and both measures were taken. Correlations were calculated separately for the three experimental data sets (Year 1 main plots, Year 1 control and defoliated plots, and Year 2 plots of all treatments). All variables except length and mortality were adjusted for differences in planting density in the intercrops.

For maize, sorghum, pumpkin, successional monocots, and successional dicots the patterns of correlation were similar: all variables except mortality and fullstandedness (and successional monocot roots) were strongly positively intercorrelated. Positive response of many variables to fertilization is probably largely responsible for the high degree of

Table 21. Correlations among maize direct productivity measures, Years 1 and 2. Experiment 1 = Year 1 main plots; 2 = Year 1 control and defoliated plots; 3 = all Year 2 plots. Values are Pearson product-moment correlation coefficients, based on all plots (of all systems and treatments) in which the measures were taken.

	EXPERIMENT	BIOMASS[a]	BIOMASS[b]	EDIBLE BIOMASS[a]	DEFOLIATED BIOMASS[c]	LAI[b]	LAI[d]	LENGTH[d]	FULLSTAND-EDNESS[e]	MORTALITY[f]
BIOMASS[b]	3	.87‡								
EDIBLE BIOMASS[a]	1	.96‡								
	2	.86‡								
	3	.97‡	.83‡							
DEFOLIATED BIOMASS[c]	2	.75‡								
	3	.79†		.52						
LAI[b]	3	.88‡	.99‡	.84‡						
LAI[d]	1	.66‡		.67‡						
	3	.82‡	.84‡	.81‡		.88‡				
LENGTH[d]	1	.53†		.74‡			.69‡			
	3	.83‡	.82‡	.76‡	.96‡	.84‡	.78‡			
FULLSTANDEDNESS[e]	1	-.36		-.29			-.01	-.24		
	3	.19	.88	.18	-.18	.13	.34	.24		

Table 21--extended.

MORTALITY[f]	1	-.42		-.47			-.22	-.10	.43		
	3	-.24	-.11	-.25	.42	-.11	-.36†	-.23	-.79‡		
ROOTS[b]	3	.89‡	.92‡	.88‡		.89‡	.72‡	.75‡	-.04	-.09	

[a]at final harvest

[b]at flowering

[c]defoliated plots only

[d]second LAI or length sample

[e]third stand count

[f]day 24-74, Year 1; day 28-96, Year 2

†significant at $p < .05$

‡significant at $p < .01$

Table 22. Correlations among sorghum direct productivity measures, Years 1 and 2. Experiment 1 = Year 1 main plots; 2 = Year 1 control and defoliated plots, 3 = all Year 2 plots. Values are Pearson product-moment correlation coefficients, based on all plots (of all systems and treatments) in which the measures were taken.

	EXPERIMENT	BIOMASS[a]	BIOMASS[b]	EDIBLE BIOMASS[a]	DEFOLIATED BIOMASS[c]	LAI[b]	LAI[d]	LENGTH[d]	FULLSTAND-EDNESS[e]	MORTALITY[f]
BIOMASS[b]	3	.77‡								
EDIBLE BIOMASS[a]	1	.90‡								
	2	.81‡								
	3	.74‡	.48†							
DEFOLIATED BIOMASS[c]	2	.43		.43						
	3	.93‡		.60						
LAI[b]	3	.87‡	.88‡	.50‡						
LAI[d]	1	.69†		.83‡						
	3	.74‡	.80‡	.36†		.78‡				
LENGTH[d]	1	.33		.60			.68†			
	3	.61‡	.77‡	.53‡	.71†	.55‡	.58‡			

Table 22--extended.

FULLSTANDEDNESS[e]	1	.78†		.54			.48	-.10		
	3	.41‡	.03	.30†	.48	.35	-.00	-.12		
MORTALITY[f]	1	-.30		-.35			-.75†	-.41	-.22	
	3	-.04	.18	-.08	-.44	.01	.24	.10	-.61‡	
ROOTS[b]	3	.70‡	.92‡	.31		.81‡	.73‡	.74‡	-.01	.24

[a]at final harvest

[b]at flowering

[c]defoliated plots only

[d]second LAI or length sample

[e]third stand count

[f]day 24-74, Year 1; day 28-96, Year 2

†significant at $p < .05$

‡significant at $p < .01$

Table 23. Correlations among cowpea direct productivity measures, Years 1 and 2. Experiment 1 = Year 1 main plots; 2 = Year 1 control and defoliated plots; 3 = all Year 2 plots. Values are Pearson product-moment correlation coefficients, based on all plots (of all systems and treatments) in which the measures were taken.

	EXPERIMENT	BIOMASS[a]	BIOMASS[b]	EDIBLE BIOMASS[a]	DEFOLIATED BIOMASS[c]	LAI[b]	LAI[d]	LENGTH[d]	FULLSTAND-EDNESS[e]	MORTALITY[f]
BIOMASS[b]	3	.29								
EDIBLE BIOMASS[a]	1	.20								
	2	.00								
	3	.75‡	-.10							
DEFOLIATED BIOMASS[c]	2	-.15		-.06						
	3	.79†		.24						
LAI[b]	3	.38	.99‡	-.03						
LAI[d]	1	.57		.37						
	3	.73‡	.88‡	.50‡		.89‡				
LENGTH[d]	1	-.12		.49			.17			
	3	.63‡	.75‡	.33‡	.75‡	.76‡	.75‡			

Table 23--extended.

FULLSTANDEDNESS[e]	1	-.40		-.44			.04	-.07		
	3	.26	.32	.21	.84‡	.31	.37†	.34†		
MORTALITY[f]	1	.40		.37			-.10	-.04	-.99‡	
	3	-.41†	-.29	-.39‡	-.50	-.27	-.51‡	-.19	-.71‡	
ROOTS[b]	3	.08	.88‡	-.23		.85‡	.69‡	.68‡	.24	-.11

[a]at final harvest

[b]at flowering

[c]defoliated plots only

[d]second LAI or length sample

[e]third stand count

[f]day 24-74, Year 1; day 28-96, Year 2

†significant at $p < .05$

‡significant at $p < .01$

Table 24. Correlations among pumpkin direct productivity measures, Years 1 and 2. Experiment 1 = Year 1 main plots; 2 = Year 1 control and defoliated plots; 3 = all Year 2 plots. Values are Pearson product-moment correlation coefficients, based on all plots (of all systems and treatments) in which the measures were taken.

	EXPERIMENT	BIOMASS[a]	BIOMASS[b]	EDIBLE BIOMASS[a]	DEFOLIATED BIOMASS[c]	LAI[b]	LAI[d]	LENGTH[d]	FULLSTAND-EDNESS[e]	MORTALITY[f]
BIOMASS[b]	3	.64‡								
EDIBLE BIOMASS[a]	3	.98‡	.64‡							
DEFOLIATED BIOMASS[c]	2	.55								
	3	.88‡		.82‡						
LAI[b]	3	.56‡	.96‡	.54‡						
LAI[d]	1	.79‡								
	3	.65‡	.96‡	.67‡		.89‡				
LENGTH[d]	1	.74†					.78†			
	3	.81‡	.91‡	.78‡	.94‡	.84‡	.92‡			

Table 24--extended.

FULLSTANDEDNESS[e]	1	-.07†					.19‡	.02‡		
	3	.34†	.62‡	.34†	.90‡	.56‡	.71‡	.52‡		
MORTALITY[f]	1	.44					.02	.14	-.15†	
	3	-.13	.02	-.06	.06	.01	-.07	-.10	-.40†	
ROOTS[b]	3	.50†	.91‡	.51†		.89‡	.92‡	.85‡	.64‡	.02

[a]at final harvest

[b]at flowering

[c]defoliated plots only

[d]second LAI or length sample

[e]third stand count

[f]day 24-74, Year 1; day 28-96, Year 2

†significant at $p < .05$

‡significant at $p < .01$

Table 25. Correlations among direct and indirect successional monocot productivity measures, Year 2. Year 1 data are omitted due to low sample size. Values are Pearson product-moment correlation coefficients, based on all plots (of all treatments) in which the measures were taken.

	BIOMASS[a]	BIOMASS[b]	LAI[c]	CANOPY COVER[c]	ROOT BIOMASS[b]	ROOT/SHOOT[b]
BIOMASS[b]	.82‡					
LAI[c]	.67‡	.90‡				
CANOPY COVER[c]	.71‡	.80‡	.79‡			
ROOT BIOMASS[b]	-.11	.25	-.01	-.17		
ROOT/SHOOT[b]	-.75‡	-.55	-.69‡	-.82‡	.65‡	
SPECIFIC LEAF MASS[b]	-.02	.01	.14	-.04	-.21	-.17

[a]at final harvest

[b]at flowering

[c]second LAI/canopy cover sample

†significant at $p < .05$

‡significant at $p < .01$

Table 26. Correlations among direct and indirect successional dicot productivity measures, Year 2. Year 1 data are omitted due to low sample size. Values are Pearson product-moment correlation coefficients, based on all plots (of all treatments) in which the measures were taken.

	BIOMASS[a]	BIOMASS[b]	LAI[c]	CANOPY COVER[c]	ROOT BIOMASS[b]	ROOT/SHOOT[b]
BIOMASS[b]	.73†					
LAI[c]	.68‡	.93‡				
CANOPY COVER[c]	.21	.51	.66‡			
ROOT BIOMASS[b]	.85‡	.61†	.61†	-.06		
ROOT/SHOOT[b]	.19	-.44	-.32	-.68†	.41	
SPECIFIC LEAF MASS[b]	.36	.19	.23	-.06	.42	.14

[a] at final harvest

[b] at flowering

[c] second LAI/canopy cover sample

† significant at $p < .05$

‡ significant at $p < .01$

intercorrelation in Year 2. Monocot roots responded little to fertilization, and that measure was uncorrelated with total biomass, LAI, and canopy cover. Sorghum and pumpkin fullstandedness were positively correlated with many other productivity variables, but maize fullstandedness was not. Mortality was consistently negatively correlated with productivity in maize and sorghum, but not in pumpkin. These relationships indicate (1) that establishment success was a factor affecting pumpkin yield, since fullstandedness but not mortality was related to yield, and (2) that death of maize and sorghum plants during the study was reflected in yield differences.

Correlations among cowpea direct productivity measures were less clear, partly because of the uniformly low yields involved. All productivity variables except fullstandedness and mortality tended to be at least weakly positively intercorrelated; the variables most strongly related to all others were LAI (second sample), length, and roots (at flowering). Cowpea mortality was significantly negatively correlated with several productivity measures in Year 2, but not Year 1, indicating that the lower levels of mortality in Year 2 were more strongly related to the yield differences found.

Correlations Among Indirect and Direct Productivity Measures

Correlations among indirect and direct productivity measures may suggest mechanisms underlying species yield differences. Correlation coefficients between the indirect productivity measures and two direct measures, edible and total aboveground biomass at harvest, were calculated for each species (Tables 25-30). Data from the three

Table 27. Correlation of maize indirect productivity measures with edible and total biomass, Years 1 and 2. Experiment 1 = Year 1 main plots; 2 = Year 1 control and defoliated plots; 3 = all Year 2 plots. Values are Pearson product-moment correlation coefficients, based on all plots (of all systems and treatments) in which the measures were taken.

	EXPERIMENT	BIOMASS[a]	EDIBLE BIOMASS[a]
COB PRODUCTION	1	.88‡	.87‡
	2	.65‡	.69‡
EDIBLE YIELD PER COB	1	.96‡	.96‡
	2	.76‡	.90‡
ROOT/SHOOT	3	.53†	.56‡
ALLOCATION RATIO	1	.60‡	.79‡
	2	.29	.70‡
	3	.53‡	.69‡
SPECIFIC LEAF MASS	3	-.05	-.10

[a] at final harvest

† significant at $p < .05$

‡ significant at $p < .01$

Table 28. Correlation of sorghum indirect productivity measures with edible and total biomass, Years 1 and 2. Experiment 1 = Year 1 main plots, 2 = Year 1 control and defoliated plots; 3 = all Year 2 plots. Values are Pearson product-moment correlation coefficients, based on all plots (of all systems and treatments) in which the measures were taken.

	EXPERIMENT	BIOMASS[a]	EDIBLE BIOMASS[a]
TILLERS	1	.46	.59
	3	.64‡	.29†
HEAD PRODUCTION	3	.80‡	.47‡
HEAD FILLING	3	-.12	.30†
EDIBLE YIELD PER HEAD	3	.38‡	.81‡
ROOT/SHOOT	3	.22	-.12
ALLOCATION RATIO	1	.04	.48
	2	-.15	.45
	3	-.10	.54‡
SPECIFIC LEAF MASS[b]	3	-.51†	-.37

[a]at final harvest

[b]at flowering

†significant at $p < .05$

‡significant at $p < .01$

Table 29. Correlation of cowpea indirect productivity measures with edible and total biomass, Years 1 and 2. Experiment 1 = Year 1 main plots; 2 = Year 1 control and defoliated plots; 3 = all Year 2 plots. Values are Pearson product-moment correlation coefficients, based on all plots (of all systems and treatments) in which the measures were taken.

	EXPERIMENT	BIOMASS[a]	EDIBLE BIOMASS[a]
THIRD-LEAF AREA	1	-.39	.15
	3	.59‡	.42‡
PODS PER PLANT	1	-.26	.47
	2	-.19	.71‡
SEADS PER POD	1	.09	.25
	2	-.25	-.26
EDIBLE SEEDS PER POD	1	.24	.20
	2	.14	.12
PERCENT EDIBLE SEEDS (By Number)	1	.25	.20
	2	.15	.14
	3	.08	.32
PERCENT EDIBLE SEEDS (By Weight)	1	-.32	.74†
	2	-.49†	.17
	3	.00	.32†
UNDAMAGED SEEDS	1	.00	.37
	2	.26	.00
	3	.17	.29†
ROOT/SHOOT	3	-.66‡	-.30
ALLOCATION RATIO	1	-.51	.73†
	2	-.59‡	.74‡
	3	.21	.67‡
SPECIFIC LEAF MASS[b]	3	-.05	.30

[a] at final harvest

[b] at flowering

† significant at $p < .05$

‡ significant at $p < .01$

Table 30. Correlation of pumpkin indirect productivity measures with edible and total biomass, Years 1 and 2. Experiment 1 = Year 1 main plots, 2 = Year 1 control and defoliated plots; 3 = all Year 2 plots. Values are Pearson product-moment correlation coefficients, based on all plots (of all systems and treatments) in which the measures were taken.

	BIOMASS[a]	EDIBLE BIOMASS[a]
FRUIT PRODUCTION	.97‡	.95‡
FRUIT WEIGHT	.65‡	.67‡
ROOT/SHOOT	-.39	-.34
ALLOCATION RATIO	.73‡	.72‡
SPECIFIC LEAF MASS[b]	.03	.00

[a]at final harvest
[b]at flowering

†significant at $p < .05$
‡significant at $p < .01$

experiments were analyzed separately. While parameters such as cob production might well be expected to be greater in plots having higher edible and total biomass, expected trends in allotment of biomass to above and belowground parts (root/shoot ratios), to reproductive and vegetative biomass (allocation ratio), and to high or low density leaves (specific leaf mass) are less clear. Correlation of these indices with productivity demonstrates the ways that biomass distribution and productivity covary, but does not necessarily imply a causal relationship (either productivity changes due to changes in the indices, or vice versa).

Maize cob production and yield per cob were positively correlated with maize edible and total biomass; sorghum tillering, head production, and edible yield per head with sorghum biomass; and pumpkin fruit production and fruit mass with pumpkin biomass. Relationships were less clear for sorghum head filling (no relation to total biomass, but positively correlated with edible biomass) and most cowpea indirect productivity measures. Cowpea third-leaf area was significantly positively correlated with biomass and edible biomass in Year 2, but not in Year 1. Cowpea edible biomass was positively correlated with number of pods per plant and percent edible seeds (by mass), but total biomass was not. Plots with higher edible and total biomass also had a higher proportion of undamaged seeds. No relationship was found between either edible or total biomass and number of edible seeds per pod, total number of seeds per pod, and percent edible seeds (by number). In the agronomic species, the relationship between root/shoot ratio and edible and total yield ranged from strongly positive (maize) to strongly

negative (cowpea, pumpkin) to neutral (sorghum). These trends are probably the result of different species' responses to fertilization; root/shoot ratio increased with fertilization in maize and sorghum and decreased in cowpea, pumpkin, successional monocots, and successional dicots.

Root/shoot ratios of both successional monocots and successional dicots were consistently negatively correlated with aboveground measures of productivity (edible and total biomass, LAI, and canopy cover), and positively correlated with root biomass. One exception was the very weak positive correlation of root/shoot ratio with total biomass in successional dicots.

In maize and pumpkin, allocation ratios were positively correlated with both edible and total biomass. More productive plants allocated a greater proportion of aboveground productivity to fruits than less productive plants. In sorghum, edible biomass was correlated with allocation ratio but total biomass was not. Cowpea allocation ratios were negatively correlated with total biomass in Year 1, but in Year 2 the correlation was slightly positive.

Specific leaf mass was uncorrelated with edible and total biomass production in maize, cowpea, and pumpkin, but was strongly negatively correlated with edible and total biomass production in sorghum. Specific leaf mass of successional dicots was weakly positively correlated with total biomass (at harvest and flowering), LAI, and root biomass. Monocot specific leaf mass, on the other hand, was not consistently positively or negatively correlated with these variables.

Summary of Year-to-Year Differences in Productivity

The LAI of all species was consistently higher in Year 1 than Year 2 (except four-crop cowpeas), but total biomass tended to be higher in Year 2 (except pumpkin and successional monocots, which were more productive in Year 1) (Table 31). Edible yield was approximately the same in the two study years for maize and sorghum; cowpea edible yield was greater in Year 2 (especially in the four-crop system), and pumpkin edible yield was higher in Year 2. Maize, sorghum, and successional monocots were the most productive species in terms of final biomass, followed by pumpkin and successional dicots. Cowpea crops failed in both years but nevertheless contributed substantial leaf area during the middle of the growing season.

Summary of System-to-System Productivity Differences

Two methods were used to compare the performance of each crop species in intercrop and monoculture in terms of several productivity measures. First, intercrop and monoculture systems were ranked by the level of each variable and the ranks summed to give an overall measure of the species' performance in different systems (Tables 32, 34, 36, and 38). Second, Yield Equivalent Ratios (YERs) were calculated for each species as the ratio of its yield in intercrop to its expected yield (based on planting density and yield in monoculture)(Tables 33, 35, 37, and 39). Yield Equivalent Ratios above one indicate greater productivity in intercrop than expected on the basis of planting density; that is, the species is more productive when planted with unlike neighbors than with an equivalent density of like neighbors.

Table 31. Summary of Year 1 and Year 2 productivity of each species. All measures are adjusted for planting density in the four-crop system. Year 1 means are from the main control plots: Year 2 means are from the control plots.

		BIOMASS[a]		EDIBLE BIOMASS[a]		LAI[b]	
SPECIES	SYSTEM	YEAR 1	YEAR 2	YEAR 1	YEAR 2	YEAR 1	YEAR 2
MAIZE	MONOCULTURE	249	244	65	62	.81	.54
	FOUR-CROP	486	517	185	170	1.18	.88
SORGHUM	MONOCULTURE	338	352	123	123	.88	.73
	FOUR-CROP	372	545	51	88	1.15	.66
COWPEA	MONOCULTURE	10	20	1	1	.42	.27
	FOUR-CROP	13	69	1	11	.25	.93
PUMPKIN	MONOCULTURE	112	52	0	26	.74	.39
	FOUR-CROP	42	2	0	0	.41	.03
MONOCOTS	SUCCESSION	283	166	--	--	.99	.61
DICOTS	SUCCESSION	42	105	--	--	1.05	.79

[a] at harvest

[b] second LAI sample in Year 2 (day 65); Year 1 LAI linearly interpolated to day 65

By the ranking method of comparing intercrop and monoculture productivity, maize adjusted productivity was clearly greater in all intercrops and the sparse maize monoculture than in the recommended-density monoculture (Table 32). Also, maize YERs in intercrop systems ranged from 0.91 to 2.34 (Table 33); all YERs except those based on defoliated leaf biomass were above one. Maize YER was highest in the maize-cowpea system, and tended to be lower in the maize-sorghum system than in other intercrops.

Sorghum productivity was also greater in intercrops than monocultures, but to a much lesser extent than maize. By all measures of productivity except length and defoliated biomass, sorghum productivity was higher in the intercrop systems than in monoculture in both study years (Tables 34 and 35). Sorghum YER was slightly above one for all measures except defoliated leaf mass.

Cowpea productivity, assessed by a number of productivity measures (Tables 36 and 37) was slightly greater in monoculture than in intercrop systems in Year 1, but was greater in the four-crop system than in monoculture in Year 2. Again, defoliated biomass and length were the rogue variables; when these two measures were removed from the analysis the systems ranked equally by cowpea productivity in Year 1, and the intercrop advantage was even more pronounced in Year 2. Cowpea YERs ranged from 0.55-1.42 in Year 1 and from 1.11-7.11 in Year 2 (excluding the defoliated leaf measure).

Pumpkin productivity was clearly lower in both the four-crop and maize-pumpkin systems than in monoculture (Tables 38 and 39). Ranks of all productivity measures except Year 1 mortality were consistently

Table 32. Summary of ranking of systems by maize productivity, Years 1 and 2. All variables except length and mortality are adjusted for planting density in the intercrop systems. Values are rankings of systems (control plots only) by each of the productivity measures. 1=highest value, except for mortality (1=lowest value).

SYSTEM	BIOMASS[a]	BIOMASS[b]	DEFOLIATED BIOMASS[c]	EDIBLE BIOMASS[a]	ROOT BIOMASS[b]	LAI[b]	LAI[d]	LENGTH[d]	MORTALITY[e]	SUMMED RANK
YEAR 1										
SPARSE MAIZE	1		2	1			2	1	1	8
MAIZE-COWPEA	2		1	2			1	3	2	11
FOUR-CROP	3		3	3			5	5	3	22
MAIZE-PUMPKIN	4		6	4			3	2	5	24
MAIZE-SORGHUM	5		5	5			4	4	6	29
MAIZE	6		4	6			6	6	4	32
YEAR 2										
FOUR-CROP	1	1	2	1	1	1	1	1	1	10
MAIZE	2	2	1	2	2	2	2	2	2	17

[a] at harvest
[b] at flowering
[c] defoliated plots only
[d] second LAI or length sample
[e] days 24-74, Year 1; days 28-96, Year 2

Table 33. Yield Equivalent Ratio (YER) of maize in intercrops, Years 1 and 2. YERs are calculated on the basis of the productivity measures listed vertically (control plots only). Asterisks indicate YERs in which numerator and denominator are significantly different by SAS Contrast procedure.

	INTERCROP SYSTEM				
YIELD PARAMETERS	MAIZE-SORGHUM (YEAR 1)	MAIZE-COWPEA (YEAR 1)	MAIZE-PUMPKIN (YEAR 1)	FOUR-CROP (YEAR 1)	FOUR-CROP (YEAR 2)
BIOMASS[a]	1.41	2.34*	1.79	1.95*	2.12*
BIOMASS[b]					1.66
DEFOLIATED BIOMASS[c]	.94	1.46	.91	1.27	.96
EDIBLE BIOMASS[a]	1.53	3.44*	2.41*	2.87*	2.74*
ROOT BIOMASS[b]					1.65*
ROOT BIOMASS[d]	1.60	.31	3.04	8.04	
LAI[b]					1.44
LAI[d]	1.29	1.63	1.38	1.08	1.61*

[a]at harvest

[b]at flowering

[c]defoliated plots only

[d]coring method, Year 1

[e]second LAI sample

Table 34. Summary of ranking of systems by sorghum productivity, Years 1 and 2. All variables except length and mortality are adjusted for planting density in the intercrop systems. Values are ranking of systems (control plots only) by each of the productivity measures. 1=highest value, except for mortality (1=lowest value).

SYSTEM	BIOMASS[a]	BIOMASS[b]	DEFOLIATED BIOMASS[c]	EDIBLE BIOMASS[a]	ROOT BIOMASS[b]	LAI[b]	LAI[d]	LENGTH[d]	MORTALITY[e]	SUMMED RANK
YEAR 1										
FOUR-CROP	1		2	2			2	3	1	11
MAIZE-SORGHUM	2		3	1			1	1	2	10
SORGHUM	3		1	3			3	2	3	15
YEAR 2										
FOUR-CROP	1	1	2	1	1	1	1	2	1	11
SORGHUM	2	2	1	2	2	2	2	1	2	16

[a]at harvest

[b]at flowering

[c]defoliated plots only

[d]second LAI or length sample

[e]days 24-74, Year 1; days 28-96, Year 2

Table 35. Yield Equivalent Ratio (YER) of sorghum in intercrops, Years 1 and 2. YERs are calculated on the basis of the productivity measures listed vertically (control plots only). Asterisks indicate YERs in which numerator and denominator are significantly different by SAS Contrast procedure.

YIELD PARAMETER	INTERCROP SYSTEM MAIZE-SORGHUM (YEAR 1)	FOUR-CROP (YEAR 1)	FOUR-CROP (YEAR 2)
BIOMASS[a]	1.04	1.10	1.55*
BIOMASS[b]			1.13
DEFOLIATED BIOMASS[c]	.77	.83	.98
EDIBLE BIOMASS[a]	1.03	1.00	1.71
ROOT BIOMASS[b]			1.01
LAI[b]			1.82*
LAI[d]	1.21	1.13	.90

[a] at harvest

[b] at flowering

[c] defoliated plots only

[d] second LAI sample

Table 36. Summary of ranking of systems by cowpea productivity, Years 1 and 2. All variables except length and mortality are adjusted for planting density in the intercrop systems. Values are rankings of systems (control plots only) by each of the productivity measures. 1=highest value, except for mortality (1=lowest value).

SYSTEM	BIOMASS[a]	BIOMASS[b]	DEFOLIATED BIOMASS[c]	EDIBLE BIOMASS[a]	ROOT BIOMASS[b]	LAI[b]	LAI[d]	LENGTH[d]	MORTALITY[e]	SUMMED RANK
YEAR 1										
FOUR-CROP	1		3	2			2	3	3	14
MAIZE-COWPEA	3		2	1			3	1	2	12
COWPEA	2		1	3			1	2	1	10
YEAR 2										
FOUR-CROP	1	1	2	1	1	1	1	2	2	12
COWPEA	2	2	1	2	2	2	2	1	1	15

[a] at harvest

[b] at flowering

[c] defoliated plots only

[d] second LAI or length sample

[e] days 24-74, Year 1; days 28-96, Year 2

Table 37. Yield Equivalent Ratio (YER) of cowpea in intercrops, Years 1 and 2. YERs are calculated on the basis of the productivity measures listed vertically (control plots only). Asterisks indicate YERs in which numerator and denominator are significantly different by SAS Contrast procedure.

YIELD PARAMETER	INTERCROP SYSTEM MAIZE-COWPEA (YEAR 1)	FOUR-CROP (YEAR 1)	FOUR-CROP (YEAR 2)
BIOMASS[a]	.89	1.27	1.11*
BIOMASS[b]			3.15
DEFOLIATED BIOMASS[c]	.86	.64*	.44*
EDIBLE BIOMASS[a]	1.42	1.16	7.11*
ROOT BIOMASS[b]			1.44
LAI[b]			3.62
LAI[d]	.79	.55	3.49

[a]at harvest

[b]at flowering

[c]defoliated plots only

[d]second LAI sample

Table 38. Summary of ranking of systems by pumpkin productivity, Years 1 and 2. All variables except length and mortality are adjusted for planting density in the intercrop systems. Values are rankings of systems (control plots only) by each of the productivity measures. 1=highest value, except for mortality (1=lowest value).

SYSTEM	BIOMASS[a]	BIOMASS[b]	DEFOLIATED BIOMASS[c]	EDIBLE BIOMASS[a]	ROOT BIOMASS[b]	LAI[b]	LAI[d]	LENGTH[d]	MORTALITY[e]	SUMMED RANK
YEAR 1										
FOUR-CROP	2		3	2.5			2	3	2	14.5
MAIZE-PUMPKIN	3		2	2.5			3	2	1	13.5
PUMPKIN	1		1	1			1	1	3	8
YEAR 2										
FOUR-CROP	2	2	2	2	2	2	2	2	2	18
PUMPKIN	1	1	1	1	1	1	1	1	1	9

[a] at harvest

[b] at flowering

[c] defoliated plots only

[d] second LAI or length sample

[e] days 24-74, Year 1; days 28-96, Year 2

Table 39. Yield Equivalent Ratio (YER) of pumpkin in intercrops, Years 1 and 2. YERs are calculated on the basis of the productivity measures listed vertically (control plots only). Asterisks indicate YERs in which numerator and denominator are significantly different by SAS Contrast procedure.

YIELD PARAMETER	INTERCROP SYSTEM: MAIZE-PUMPKIN (YEAR 1)	FOUR-CROP (YEAR 1)	FOUR-CROP (YEAR 2)
BIOMASS[a]	.41*	.37*	.04
BIOMASS[b]			.02*
DEFOLIATED BIOMASS[c]	.83	.59*	.08
EDIBLE BIOMASS[a]			0
ROOTS[b]			.19*
LAI[b]			.02*
LAI[d]	.50*	.58	.08*

[a] at harvest

[b] at flowering

[c] defoliated plots only

[d] second LAI sample

higher in monoculture than in the intercrops, and pumpkin YERs ranged from 0-0.83; most were less than 0.50.

Summary of Response to Stress Treatments

The four agronomic species all responded positively to fertilization; maize and sorghum responded more strongly than cowpea and pumpkin (Table 40). None of the agronomic species responded with significant mortality differences, however. Successional monocots, but not successional dicots, were also stimulated by fertilization.

Cowpea was the only species to respond to pesticide spraying (Table 41). Watering seemed to increase cowpea productivity (Table 42), but this, as well as the cowpea response to defoliation, may have been due to abnormally low productivity in cowpea plots. Sorghum total biomass was significantly decreased by defoliation, but edible biomass was not. No other significant defoliation effects were found (Table 43).

There were no clear differences in species response to the stress treatments in simple and diverse systems, except that pumpkin productivity was more highly stimulated by fertilization in monoculture than in the four-crop system.

Discussion

Comparison with Regional Yields

Yields of maize and sorghum agreed with those of Tanzania as a whole and other experimental estimates of yields under local farming conditions. Edible maize yields of 65 and 62 g/m^2 (Year 1 and Year 2

Table 40. Summary of effects of fertilization on productivity of each species in various sytems, Year 2. + = significantly higher biomass, root mass, LAI, length, or mortality in fertilized plots than controls; 0 = no significant difference. Duncan's tests were performed on samples of all systems combined, but are reported separately for each system here, for the sorghum edible and total biomass data.

SPECIES	SYSTEM	BIOMASS[a]	BIOMASS[b]	EDIBLE BIOMASS[a]	ROOT BIOMASS[b]	LAI[b]	LAI[c]	LENGTH[c]	MORTALITY[d]
MAIZE	FOUR-CROP	+	+	+	+	+	+	+	0
	MONOCULTURE	+	+	+	+	+	+	+	0
SORGHUM	FOUR-CROP	+	+	0	+	+	+	+	0
	MONOCULTURE	+	+	0	+	+	+	+	0
COWPEA	FOUR-CROP	0	0	0	+	+	+	+	0
	MONOCULTURE	0	0	0	+	+	+	+	0
PUMPKIN	FOUR-CROP	0	0	0	0	0	0	+	0
	MONOCULTURE	+	0	+	0	0	0	+	0
MONOCOTS	SUCCESSION	+	+		0		+		
DICOTS	SUCCESSION	0	0		0		0		

[a]at harvest

[b]at flowering

[c]second LAI/length sample

[d]day 28-96

Table 41. Summary of effects of pesticide spraying on productivity of each species in various systems, Year 2. + = significantly higher biomass, LAI, length, or mortality in sprayed plots than controls; - = significantly lower in sprayed plots than controls; 0 = no significant difference. Duncan's tests were performed on samples of all systems combined, but are indicated separately for each system here, for the sorghum edible and total biomass data.

SPECIES	SYSTEM	BIOMASS[a]	EDIBLE BIOMASS[a]	LAI[b]	LENGTH[b]	MORTALITY[c]
MAIZE	FOUR-CROP	0	-	0	0	0
	MONOCULTURE	0	0	0	0	0
SORGHUM	FOUR-CROP	0	0	0	0	0
	MONOCULTURE	0	0	0	0	0
COWPEA	FOUR-CROP	+	+	+	+	-
	MONOCULTURE	+	+	+	+	-
PUMPKIN	FOUR-CROP	0	0	0	0	0
	MONOCULTURE	0	0	0	0	0
MONOCOTS	SUCCESSION	0		0		
DICOTS	SUCCESSION	0		0		

[a] at harvest

[b] second LAI/length sample

[c] day 28-96

Table 42. Summary of effects of watering on productivity of each species in various systems, Year 2. + = significantly higher biomass, length, or mortality in watered plots than controls; - = significantly lower in watered plots than controls; 0 = no significant difference. Duncan's tests were performed on samples of all systems combined, but are reported separately for each system here, for the sorghum edible and total biomass data.

SPECIES	SYSTEM	BIOMASS[a]	EDIBLE BIOMASS[a]	LENGTH[b]	MORTALITY[c]
MAIZE	FOUR-CROP	0	0	0	0
	MONOCULTURE	0	0	0	0
SORGHUM	FOUR-CROP	0	0	0	0
	MONOCULTURE	0	0	0	0
COWPEA	FOUR-CROP	0	0	0	-
	MONOCULTURE	0	+	0	-
PUMPKIN	FOUR-CROP	0	0	0	0
	MONOCULTURE	0	0	0	0
MONOCOTS	SUCCESSION	0			
DICOTS	SUCCESSION	0			

[a] at harvest

[b] second length sample

[c] day 28-96

Table 43. Summary of effects of defoliation on productivity of each species in various systems, Years 1 and 2. – = significantly lower biomass, length, or mortality in defoliated than control plots; 0 = no significant difference. Duncan's tests were performed on samples of all systems combined, but are indicated separately for each system here, for the following measures: maize edible and total biomass (Year 1); sorghum edible biomass (Year 1); cowpea edible and total biomass (Year 1); pumpkin edible and total biomass (Year 1); sorghum edible and total biomass (Year 2).

SPECIES	SYSTEM	YEAR	BIOMASS[a]	EDIBLE BIOMASS[a]	LENGTH[b]	MORTALITY[c]
MAIZE	FOUR-CROP	1	0	0		
		2	0	0	0	0
	MAIZE-SORGHUM	1	0	0		
	MAIZE-COWPEA	1	0	0		
	MAIZE-PUMPKIN	1	0	0		
	SPARSE MAIZE	1	0	0		
	MONOCULTURE	1	0	0		
		2	0	0	0	0
SORGHUM	FOUR-CROP	1	–	0		
		2	–	0	0	0
	MAIZE-SORGHUM	1	0	0		
	MONOCULTURE	1	0	0		
		2	–	0	0	0
COWPEA	FOUR-CROP	1	0	0		
		2	0	0	0	–
	MAIZE-COWPEA	1	0	0		
	MONOCULTURE	1	0	0		
		2	0	0	0	–
PUMPKIN	FOUR-CROP	1	0	0		
		2	0	0	0	0
	MAIZE-PUMPKIN	1	0	0		
	MONOCULTURE	1	0	0		
		2	0	0	0	0
MONOCOTS	SUCCESSION	1	0			
		2	0			
DICOTS	SUCCESSION	1	0			
		2	0			

[a]at harvest

[b]second length sample

[c]day 24-74, Year 1; day 28-96, Year 2

means in control plots) in recommended-density maize monoculture agreed with the national average of 75 g/m^2 (Fortmann 1976) and 67 g/m^2 (Acland 1975). Serena-variety sorghum can yield up to 340-450 g/m^2 with improved husbandry in Tanzania (Acland 1975) but regional averages of 170 g/m^2 (Doggett and Jowett 1966, from 33 East African lowland trials), 65-75 g/m^2 (Purseglove 1972) and 55-170 g/m^2 (Acland 1975) are more realistic for local farming conditions. Sorghum yield in this study averaged 123 g/m^2 in control plots in both years, indicating that the site and weather during the study were moderately favorable for sorghum.

Tanzanian experiment station cowpea trials yielded an average of 4-95 g/m^2 and 23 village trials yielded an average of 85 g/m^2 without pesticide (Brockman 1978). Other regional estimates of cowpea yield are 40-60 g/m^2 (Purseglove 1974, for the tropics as a whole) and 34-45 g/m^2 (Acland 1975, for East Africa). Cowpea yields of 1 g/m^2 in this study constituted crop failures due to insect and disease attack. Data on pumpkin yields in Tanzania were not available, but Purseglove (1974) estimated average tropical pumpkin yields at 200 g/m^2 dry fruit; pumpkin in this study yielded a maximum of 26 g/m^2. The low yields were probably caused by pest attack in both years, since vegetative growth did occur.

Growth of successional vegetation of 326 and 271 g/m^2 in approximately 150 days in Years 1 and 2 was within the range expected for wet season growth in the dry tropics. Data are not available from comparable sites in Africa, but Caribbean-area dry forest sites produced 143 and 194 g/m^2 of biomass in approximately 170 days of wet season regrowth (Ewel 1971). The rate of succession at the Morogoro site was below that reported for moister sites in Central America (> 2000 m rainfall) of

405 g/m^2 in 120 days (Harcombe 1977) and 750 g/m^2 in one year (Snedaker 1980). Reduced successional regrowth in the second year of this study implies slower rates of recovery of natural vegetation after more than one year of soil cultivation, an occurrence that is often attributed to degradation of soil resources and seed stores.

The productivity of successional vegetation was higher than that of all agricultural systems by several measures. The high LAI and canopy cover of successional vegetation were particularly notable, and suggest that this is one area in which the agricultural systems might be improved. Differences in total biomass between the successional and agricultural systems were not as dramatic as the differences in LAI and canopy cover. LAI declined relatively early in the growing season in the two most productive systems, successional vegetation and sorghum monoculture; higher productivity per day over a shorter growing season may be the most successful strategy in the Morogoro environment. The current search for a more rapidly-maturing maize variety is in line with this idea, and will improve the match between agricultural system function and that of natural succession.

Food Yield as a Measure of Productivity

The poor correlation of edible yield with other measures of productivity in some species in this study shows that edible yield is not a reliable indicator of overall system productivity. Pest activity, in particular, can reduce edible yield but not total yield. Care should be taken when drawing conclusions about competitive relations and ecosystem productivity, especially, based on edible yields alone.

Unless the sole purpose of the study is to measure food production, other measures that relate more directly to productivity (such as total biomass, root biomass, and LAI) should also be used.

Absolute Comparisons Among Systems

If the goal of agricultural development were to maximize edible or total biomass harvest without regard to nutritional composition of the yield, the results of this study would suggest maize or sorghum monocultures as systems of choice for the Morogoro area. All of the agricultural systems studied that contained monocots were consistently more productive than the two dicot monocultures (cowpea and pumpkin). The dicots used in the study were widely planted in the Morogoro area but appeared to be susceptible to crop failure. While the relative abundance of monocots in the systems studied was positively correlated with total biomass, it was negatively correlated with LAI and canopy cover. This suggests that monocots may be stronger than dicots as biomass producers, while dicots are more important in terms of LAI and canopy cover production. Pumpkin LAI was notably high in relation to its biomass, and presence of cowpeas in intercrops was associated with weed suppression (compared with corresponding monocultures).

Successional vegetation contained approximately equal proportions of monocots and dicots, unlike the mixed monocot-dicot agricultural systems, which tended to develop greater monocot leaf area (percent monocot LAI) than expected by the planting proportions. Emphasis on monocots in agricultural systems may be more appropriate under fertilized conditions, where the composition of both the succession

system and the mixed monocot-dicot intercrops heavily favored monocots.

Comparison of Intercrops with Corresponding Monocultures

Intercrop systems were shown to consistently yield more per unit land area than the same area divided among monocultures of their component species. The YER of the four-crop intercrop, based on edible yield, was 1.64 and 2.08 in Years 1 and 2, which means that a farmer planting 1 ha to the intercrop would harvest 64-103 percent more edible biomass than if the area were divided into four 1/4-ha monocultures of maize, sorghum, cowpea, and pumpkin. A high diversity of cultivated species is normally needed by subsistence farmers for nutritional reasons: this result shows that spatially mixing those species gives very substantial increases in productivity

The greater edible and total biomass at harvest from intercrops than from monocultures corroborates Trenbath's (1974) finding that yield of two-crop systems usually exceeds the mid-monoculture yield. Unfortunately, the substitutive method was used to determine planting densities in those studies, so yield increases may have been due to either spatial mixing or to increased overall planting density. The results from this study are new because (1) overall functional planting density was controlled, so the yield increase was due only to effects of increased spatial diversity, (2) a diverse four-crop system typical of local cropping systems was used, (3) the productivity advantage was shown for variables other than edible and total aboveground biomass, and

(4) the productivity advantage was shown to occur under fertilized, sprayed, and watered conditions (but not defoliated conditions) as well as in a control treatment that imitated local farming practices.

Productivity differences between intercrops and corresponding monocultures were due to increased productivity per plant and changes in biomass distribution, rather than mortality differences among systems. Fullstandedness of the intercrop systems was approximately equal to that of corresponding monocultures. Nevertheless, high mortality of one species in an intercrop was "diluted" by the presence of other species with lower mortality, resulting in stands of consistent, intermediate fullstandedness, a feature that may optimize resource use.

Response to the Stress Treatments

Maize and sorghum response to nitrogen and phosphorus in Tanzania, but not to potassium, is well documented (Anderson 1963, LeMare 1970, Purseglove 1972, Acland 1975). Maize responded more dramatically to fertilization in this study than in other Tanzanian studies (150 g/m^2 increase versus 80 and 30-100 g/m^2 increases by Scaife 1968, Anderson 1969), reflecting the poor nutrient status of the soil. Pumpkins were also reported to respond to nitrogen and phosphorus fertilization (Purseglove 1974) but local data were not available. Cowpea response to phorphorus has been reported (Acland 1975) but low response to nitrogen is expected due to cowpea's ability to fix nitrogen. Fertilization in this study raised successional aboveground biomass from 270 to 395 g/m^2 (approximately 45 percent); in a wetter site in Costa Rica, a comparable increase of 50 percent in a 120-day period has been reported

(Harcombe 1977). Greater monocot than dicot response to fertilization was found both in successional systems and in the four-crop system. Greater response of monocots than dicots to fertilizer was also found in mixed grass-legume pastures (Donald 1963).

Rainfall was adequate during both study years to maintain soil moisture at nearly field capacity almost until harvest. The low degree of moisture stress in the study years accounts for the low response to the watering treatment. Coincidental, random placement of control cowpea monoculture plots in unusually wet areas may account for the slightly higher cowpea productivity in watered plots than controls.

The combination of diazinon, dimecron, and copper sulfate used in the pesticide treatment should have given broad protection against many (but not all) pests and fungal diseases (Bohlen 1978). The low response of maize and sorghum to spraying can be interpreted to mean that those crops were not seriously limited by pests and diseases. Slight phytotoxic effects of spraying were seen in the negative response of pumpkin, and possibly maize, by some productivity measures. The positive response of cowpeas to pest control was not surprising; large responses to spraying have been reported in Tanzania, and a substantial proportion of research on grain legumes in Tanzania concerns pest control (Brockman 1978).

A large body of literature exists concerning the feedback (or "regulatory") effects of defoliation and insect damage on system productivity (see review by McNaughton 1979). Several mechanisms may operate to stimulate productivity (i.e., recovery) after leaf damage, including increased photosynthesis in remaining leaves (Wareing et al.

1968, Detling et al. 1979), changes in abiotic fluxes such as nutrients (Mattson and Addy 1975), and release of lateral buds (Harris 1974). Several researchers (Rhodes 1970, Trenbath 1974, Rudd et al. 1976) suggest that the rate of response is primarily a function of the remaining leaf area.

All systems in this study were very resilient with respect to defoliation, although the maize-pumpkin system did not fully recover and productivity of the maize-cowpea and succession systems appeared to be stimulated by defoliation. The resilience of cowpea after defoliation has been noted previously (Acland 1975). It is likely that in agricultural systems, responses to defoliation are more related to individual species' responses and to the timing of defoliation than to a generalized system property such as residual LAI.

Defoliation had little effect on either edible or total biomass; the treatment was not severe enough to significantly reduce productivity. The suggestion by Rockwood (1973) that reproductive activity is curtailed by defoliation was therefore not confirmed. Allocation ratios were generally lower under conditions of low productivity, however, supporting the idea that reproductive activity declines with increasing intensity of stress.

Effects of the Stress Treatments on Intercrop Advantage

If stressors interact multiplicatively upon productivity, as suggested by Lugo (1978) and Odum (1971), greater response to changes in competition (intercropping) is expected at high than at low intensities of stress. YER should be highest in the least productive

stress treatment, and lowest in the most productive treatment. Consistent with this reasoning, YER was higher in control plots than in fertilized plots. Yield Equivalent Ratio was also lower in pesticide-sprayed plots than controls, although spraying did not have a clear positive effect on yield. Yield Equivalent Ratio was approximately equal in watered plots and controls, as expected since the watering treatment did not affect productivity. Reduced intercrop advantage with defoliation in the Year 2 four-crop system (YER approximately equal to one) does not conform with the prediction of greater intercrop advantage at high levels of stress. In Year 1, also, the results seem to contradict the hypothesis; YER increased with defoliation in systems in which productivity was stimulated (maize-cowpea), and decreased with defoliation in systems with reduced productivity (maize-pumpkin). One may question whether the 50 percent defoliation treatment constituted a significant stress, however, since productivity was in general not significantly affected.

Rhodes (1970) also found reduced intercrop advantage under a frequent cutting regime. Trenbath (1974) suggested that reduced intercrop advantage in defoliated intercrops may be due to reduction of those productivity advantages related to leaf area and leaf angle distribution throughout the canopy.

Stress and Biomass Distribution

Root/shoot ratios tended to decrease as productivity increased (reduced stress), whereas allocation ratios increased in response to reduced stress. Several lines of evidence support these statements,

including correlations of root/shoot and allocation ratios with biomass (analyzed both across systems and for each species); comparisions of control and fertilized plots; comparison of (productive) monocots with (less productive) dicots; year-to-year comparisons; and comparisons of each species' root/shoot and allocation ratios under varying levels of stress from competition.

All crops did not strictly conform to the generalization that allocation ratios increase with increasing productivity, however. Year 1 cowpea yield was uniformly low in all plots, resulting in low allocation ratios even for those plots having slightly higher biomass production. Cowpea seed production may have been too severely limited by pests in Year 1 to show the expected correlation of allocation ratio with biomass. Sorghum allocation ratio was not strongly correlated with total biomass, but was strongly correlated with edible yield, edible yield per head, and head fullness ($p < .01$), and strongly negatively correlated with tillering ($p < .01$). Tillering was strongly correlated with frequency of both shootfly and stalk borer damage ($p < .01$), and was significantly greater in the four-crop system than in monoculture (as was the shootfly) and significantly greater in fertilized than control plots (as was the stalk borer). Regardless of whether pest attack can be conclusively cited as the cause of tillering, the ramifications of tillering seem clear: increased head production ($p < .01$), increased LAI ($p < .01$ at flowering and second LAI sample), decreased specific leaf mass ($p < .01$) and increased edible and total biomass production ($p < .05$). Stimulation of leaf and head production in tillered plants under productive conditions appears to be responsible for the low

correlation of sorghum allocation ratio with total biomass and its negative correlation with tillering and head production.

Specific leaf mass was not, in general, significantly related to productivity. A few interesting exceptions to this generalization were found, however. Sorghum specific leaf weight was significantly negatively correlated with productivity in a sample of all systems and treatments combined and was significantly higher in the four-crop intercrop than in monoculture. This may have been due to increased tillering in the four-crop system and in fertilized plots (where specific leaf mass was nonsignificantly higher than in controls). Maize, cowpea, and pumpkin specific leaf mass were also lower in intercrop than monocultures, possibly because of increased leaf expansion due to shading. Slight positive correlation of dicot specific leaf mass with both dicot productivity and canopy cover also suggests a possible shading effect; shading by monocots may reduce both dicot productivity and specific leaf mass. The negative correlation of dicot specific leaf mass and monocot LAI ($r = -.21$ for all plots, $r = -.41$ when fertilized plots are excluded) supports the supposition that shading was the cause of reduced dicot specific leaf mass. Pumpkin specific leaf mass was significantly lower in fertilized than control plots; sorghum and cowpea leaves were also lighter in fertilized plots, but no clear trends were found for maize, successional monocots, or succession dicots. In each of the above examples of reduced specific leaf mass associated with increased productivity, increased LAI could feed back to further increase productivity.

Although the physiological basis for changes in root/shoot ratio, allocation ratio, and specific leaf mass are complex and will not be discussed here, the implications of the changes in bomass distribution that are associated with changes in productivity are interesting. Increased productivity in intercropping systems is channelled more into aboveground biomass than belowground biomass, and a greater proportion of that aboveground biomass is channelled into edible yield (seed production). Greater LAI increases than expected may also occur due to reduced leaf mass per unit area and feed back to stimulate productivity. By these mechanisms, rather small changes in competition and resource use could result in larger differences in edible and total yield. Trenbath (1974) suggested that higher allocation ratios could account for intercrop/monoculture differences in food production; the results from this study indicate that changes in root/shoot ratios, allocation ratios, and specific leaf mass may all contribute to greater intercrop advantage in terms of edible yield than in terms of total yield. The exaggeration of edible yield differences was clearly shown by the consistently higher YERs based on edible yield than those based on total yield.

Species YER as a Measure of Competitiveness and Aggressiveness

The ratio of each species' yield in monoculture to its expected yield, based on planting density and yield in monoculture (species YER) should be interpreted carefully. Yield Equivalent Ratios above one can result from resource partitioning, compensatory growth, or other biotic or abiotic interactions that may influence productivity. If

a species YER above one is to be interpreted to mean that interspecific competition is less than intraspecific competition for the species and system in question, the meaning of "competition" must be broad enough to encompass these various mechanisms.

The usual situation in an intercrop is that some species perform better in the intercrop (the "aggressors") while others are more productive in monocultures (the "subordinates")(Trenbath 1974). It should be emphasized that the terms "aggressive" and "subordinate" refer to a species' role in a specific community rather than its innate capacity for growth and acquisition of resources. When unlike neighbors reduce a species' productivity less than does an equal density of like neighbors, the species is called an aggressor; in a different system the same species could function as a subordinate. In actuality, a given species is likely to fill the same role in many types of communities due to its innate resource-acquiring characteristics.

Maize YER was highest in the maize-cowpea intercrop, indicating low cowpea competitiveness with maize. Cowpea's low competitiveness with maize was also indicated by the nearly equal yield of maize in the maize-cowpea and sparse maize systems, in which the planting densities of maize were equal. Sorghum, on the other hand, competed almost as strongly with maize as other maize plants did. Maize was therefore less aggressive in the maize-sorghum system than in the other intercrops, particularly the maize-cowpea system.

Sorghum was also an aggressor in all intercrops, but less so than maize. Cowpea was an aggressor in the four-crop system in Year 2, but was

neither an aggressor nor a subordinate in Year 1, when factors other than competition for growth factors (e.g., uniformly high levels of pests and diseases) may have equalized cowpea yields among systems. The subordinate role of pumpkin in intercrops (indicated by YERs consistently less than one) is likely due to competition for light, water, and nutrients rather than differences in pest and disease levels.

At the end of the study, it was learned that local farmers often plant pumpkins in the early stages of field preparation, several days to several weeks before other species are planted. It is possible that in such systems all species can act as aggressors, having greater productivity than when grown as monocultures. In this study, the negative effect of aggressive neighbors on pumpkin was more than offset by increased productivity of the other three species, resulting in increased total productivity.

Competitive interactions in the four intercrop systems in this study were all different (Table 44), but all systems had higher productivity than their corresponding monocultures. It is particularly noteworthy that in two intercrop systems (maize-sorghum and maize-cowpea) there was no subordinate species; both elements of the mixture performed at least as well as in monoculture.

McGilchrist's (1965) "aggressivity" and Willey and Rao's (1980) "competitive ratio" can be translated in terms of species YERs. "Aggressivity" is the difference in 2 species' YERs in intercrop, while "competitive ratio" is the ratio of 2 species' YERs. Subtraction and division are used to compare the YER's; the implication is that the <u>relative</u> aggressiveness of two species is the property of interest.

Table 44. Competitive interactions in four intercrop systems. Symbols (0, +, -) refer to a species' productivity in intercrop compared with that in monocultures, based on YERs by several productivity measures. 0 = no difference in species productivity in intercrop and monoculture, + = increased productivity in intercrop; - = decreased productivity in intercrop.

SYSTEM	MAIZE	SORGHUM	COWPEA	PUMPKIN	OVERALL SYSTEM YIELD
MAIZE-SORGHUM	+	+			+
MAIZE-COWPEA	+		0		+
MAIZE-PUMPKIN	+			-	+
FOUR-CROP	+	+	+/0	-	+

The relative aggressiveness of two species can perhaps be more directly compared by simple comparisions of the species' YERs. In this study, for example, maize YER (based on edible yield) was 2.74 in the four-crop system (Year 2), while that of sorghum was 1.71. There is no need to calculate the difference or ratio of YERs to determine that maize is more aggressive than sorghum. Furthermore, such calculations infer that one species is subordinate, whereas in this case both species are aggressors, but to differing degrees. The application of the "aggressivity" and "competitive ratio" calculations to intercrops containing more than two species has also not been clarified.

Height and aggressiveness

Trenbath (1974) suggests that canopy height and investment in stems increase a species' aggressiveness in intercrops. That generalization held true in this study; maize was the tallest species and also the most aggressive, while pumpkin leaves were located lowest in the canopy and that species was subordinate in intercrops. Sorghum and cowpea, in addition to being generally shorter than maize, also did not tend to respond with increased height growth to conditions that generally stimulated productivity. Fertilization did increase the height of both species somewhat, but both cowpea and sorghum were taller in monoculture than in the more productive four-crop system in both study years. Maize, in contrast, responded with considerable height growth to both reduced competition (substitution of other species for maize in the intercrop systems) and improved resource availability (fertilization). Pumpkin productivity differences were also highly correlated

with length, but pumpkin stems grow along the ground, so length growth would not increase competitiveness with respect to taller species.

CHAPTER FOUR
YIELD STABILITY

Introduction

Yield stability was measured by the coefficient of variation of yield measures or by the percent yield response to changes in stress intensity (in the stress treatments). Stability was evaluated first on the system level. Year-to-year and plot-to-plot variability of system yield were measured and responsiveness to each of the stress treatments evaluated. Yield stability at each intensity of stress was also assessed. System response to varying levels of packing (competition) was also evaluated, where possible, and discussed. Interactions among stressors on the system level was examined by comparing the yield advantage of intercropping (effects of reduced competition) at several intensities of stress. Yield stability of each species was also evaluated by year-to-year and plot-to-plot fluctuations, responsiveness to the stress treatments, and responsiveness to changes in competition (intercropping). Possible reasons for differences in system stability in intercrops and monocultures are discussed, including a model of effects of one or more stressors on stability, based on Michaelis-Menton limiting factor response equations.

Results

System Stability

Year-to-year fluctuations

Year-to-year variability of five productivity measures (Table 45) was clearly lowest in sorghum monoculture, although both maize and sorghum gave stable edible and total biomass yields over the two study years. Successional vegetation and the four-crop system were also relatively stable; the cowpea and pumpkin system varied quite widely from year to year. The coefficient of variation of the five measures ranged from 0.31 to 1.41 in those two crops. The four-crop system varied slightly less from year to year than did corresponding monocultures.

Plot-to-plot variability within years

Overall constancy of the systems within years (all treatments combined, Tables 46 and 47) was also greatest in the sorghum and four-crop systems and lowest in cowpea and pumpkin monocultures. The maize-sorghum system (Year 1) was nearly as stable as the four-crop system, but the other two-crop systems (maize-cowpea and maize-pumpkin) and the sparse maize monoculture were among the least stable. In both Years 1 and 2 maize productivity varied considerably among plots (unlike year-to-year variability), largely an indication of its response to the fertilizer treatment. Point-to-point (plot-to-plot) variability of intercrops and corresponding monocultures within years

Table 45. Summary of year-to-year stability of system productivity by several measures. CV = coefficient of variation between Year 1 and Year 2 means (control plots only). Variability is also given for corresponding monocultures of the four-crop system. Rank of 1 = lowest variability (highest stability).

SYSTEM	BIOMASS[a] CV	BIOMASS[a] RANK	EDIBLE BIOMASS[a] CV	EDIBLE BIOMASS[a] RANK	LAI[b] CV	LAI[b] RANK	CANOPY COVER[b] CV	CANOPY COVER[b] RANK	FULLSTAND-EDNESS[c] CV	FULLSTAND-EDNESS[c] RANK	SUMMED RANK[d]	SUMMED RANK[d]
MAIZE	.01	1	.03	2	.28	5	.13	3	.03	1.5	12.5	9
SORGHUM	.03	2	0	1	.13	2	.07	1	.05	3	9	5
COWPEA	.47	6	.55	5	.31	6	.40	6	.33	5	28	18
PUMPKIN	.51	7	1.41	6	.44	7	.53	7	.49	6	33	21
FOUR-CROP	.15	5	.10	3	.11	1	.22	4	.10	4	17	10
CORRESPONDING MONOCULTURES	.04	3	.08	4	.27	4	.26	5	.03	1.5	17.5	12
SUCCESSION	.13	4	--	--	.26	3	.09	2	--	--	--	9

[a]at harvest

[b]second LAI/canopy cover sample in Year 2 (day 65); Year 1 LAI/canopy cover linearly interpolated to day 65

[c]third stand count in Year 1 (day 75); Year 2 stand count lineraly interpolated to day 75

[d]all variables

[e]biomass, LAI, and canopy cover only

Table 46. Yield stability among plots, Year 1. Values are coefficients of variation of each measure among plots (n = 6, a sample of control and defoliated plots combined) and rankings of the systems by the stability of each measure (in parentheses). 1 = lowest coefficient of variation (most constant).

SYSTEM	BIOMASS[a]	EDIBLE BIOMASS[a]	SUMMED RANK
MAIZE	25.2 (6.5)	28.2 (5)	5
SPARSE MAISE	36.4 (9)	32.6 (7)	7.5
SORGHUM	17.3 (1)	15.6 (1)	1
COWPEA	20.3 (4)	32.2 (6)	4
PUMPKIN	25.2 (6.5)	-- --	--
MAIZE-SORGHUM	19.0 (3)	25.1 (4)	3
MAIZE-COWPEA	28.5 (8)	40.4 (8)	7.5
MAIZE-PUMPKIN	41.6 (10)	20.8 (2)	6
FOUR-CROP	18.1 (2)	21.1 (3)	2
SUCCESSION	21.1 (5)	-- --	--

[a]at final harvest

Table 47. Yield stability among plots, Year 2. Values are coefficients of variation of each measure among plots (n=9-25, mean=18, a sample of all treatments combined) and rankings of the systems by the stability of each measure (in parentheses). 1=lowest coefficient of variation (most constant).

SYSTEM	BIOMASS[a] (A)	BIOMASS[b] (B)	EDIBLE BIOMASS[a] (C)	ROOTS[b] (D)	LAI[c] (E)	CANOPY COVER[c] (F)	FULLSTAND-EDNESS[d] (G)	SUMMED RANK (A+B+D+E+F)	SUMMED RANK (ALL VARIABLES)
MAIZE	62.9 (4)	59.0 (4)	85.8 (3)	69.0 (4)	65.6 (4)	51.3 (4)	12.8 (1.5)	4	3
SORGHUM	38.5 (1)	47.0 (2)	43.5 (1)	52.3 (2)	35.5 (2)	24.0 (2)	12.8 (1.5)	1	1
COWPEA	72.0 (5)	143.2 (6)	112.8 (4)	82.5 (5)	81.3 (5)	68.6 (5)	13.7 (3)	5	4
PUMPKIN	136.8 (6)	115.0 (5)	171.2 (5)	105.1 (6)	141.8 (6)	127.6 (6)	77.6 (5)	6	5
FOUR-CROP	42.2 (2)	42.0 (1)	52.3 (2)	53.1 (3)	32.0 (1)	31.6 (3)	14.6 (4)	2	2
SUCCESSION	42.6 (3)	54.3 (3)	-- --	51.0 (1)	51.1 (3)	12.7 (1)	-- --	3	--

[a] at final harvest
[b] at flowering
[c] second LAI/canopy cover sample
[d] third stand count

could not be compared because the monocultures were not paired in the experimental design.

Responsiveness to the stress treatments

Effects of each stress treatment on system yield were analyzed as a measure of system stability with respect to different types of stressors. As discussed earlier, only the fertilization treatment had consistent significant effects on yield. In Tables 48 and 49 the effects of the stress treatments are expressed both as absolute change from controls and percent change from controls. The latter is the better measure of system stability because it expresses response in relation to biomass.

Cowpea was the least stable system with respect to fertilization (102 and 345 percent change in biomass and LAI from controls), but this may have been biased by unusually low control plot yields. Maize and successional vegetation were also very responsive to added nutrients (110 to 178 percent change in biomass and LAI from controls). Pumpkin was responsive in terms of biomass (especially edible biomass), but not in terms of LAI. The four-crop system and sorghum monoculture were both stable with respect to nutrient level, and the four-crop system was more stable than corresponding monocultures.

Defoliation significantly decreased biomass in the maize-pumpkin system in Year 1, but had no significant effect on harvest biomass for any other system. Early timing of defoliation in Year 1 may have been responsible for its overall negative effect on system productivity; when defoliation was performed later in the growing season, in Year 2, it stimulated productivity in four out of six systems. Greater resilience

Table 48. System stability with respect to defoliation, Year 1. Effects of defoliation are given as both absolute change and percent of control, and are also shown for the corresponding monocultures of intercrop systems. Asterisk indicates significant difference from controls.

	EFFECT OF DEFOLIATION ON TOTAL ABOVEGROUND BIOMASS	
SYSTEM	g/m^2	% CONTROL
MAIZE	-45	-22
SPARSE MAIZE	-19	-10
SORGHUM	-28	-11
COWPEA	- 0.4	-5
PUMPKIN	-11	-8
MAIZE-SORGHUM	-11	-5
CORRESPONDING MONOCULTURES	-37	-16
MAIZE-COWPEA	41	21
CORRESPONDING MONOCULTURES	-23	-22
MAIZE-PUMPKIN	-176	-50*
CORRESPONDING MONOCULTURES	-33	-19
FOUR-CROP	-43	-20
CORRESPONDING MONOCULTURES	-22	-14
SUCCESSION	3	2

Table 49. System stability with respect to fertilization, spraying, defoliation, and watering, Year 2. Effects of the treatments are given as both absolute change and percent of control, and are also shown for corresponding monocultures of intercrop systems. Asterisks indicate significant differences from controls.

TREATMENT EFFECT ON
TOTAL ABOVE GROUND BIOMASS, COMPARED WITH CONTROL

	FERTILIZED		PESTICIDE		DEFOLIATED		WATERED	
SYSTEM	g/m^2	%	g/m^2	%	g/m^2	%	g/m^2	%
MAIZE	435	178*	1	0	53	22	2	1
SORGHUM	201	57*	3	1	-40	-11	-106	-30
COWPEA	20	102	91	466	46	234	35	178
PUMPKIN	127	243*	-45	-87	12	24	-28	-53
FOUR-CROP	194	68*	-34	-12	-105	-37	-48	-17
CORRESPONDING MONOCULTURES	196	117	12	7	13	8	-24	-14
SUCCESSION	326	120	120	44	87	32	12	4

TREATMENT EFFECT ON LAI,
COMPARED WITH CONTROL

	FERTILIZED		PESTICIDE	
SYSTEM	AMOUNT	%	AMOUNT	%
MAIZE	.60	100*	-.17	-31
SORGHUM	.38	52	.04	6
COWPEA	.92	345*	1.36	508*
PUMPKIN	.06	14	-.33	-85
FOUR-CROP	.39	62	.26	41
CORRESPONDING MONOCULTURES	.48	100	.23	48
SUCCESSION	1.90	130*	-.09	-6

Table 50. Yield stability in each of five treatments, Year 2. Values are the coefficients of variation of each measure among plots (n=20-39, mean=28, a sample of all systems combined) and rankings of the treatments by the stability of each measure (in parentheses). 1=lowest coefficient of variation (most constant).

TREATMENT	BIOMASS[a] (A)	BIOMASS[b] (B)	EDIBLE BIOMASS[a] (C)	ROOTS[b] (D)	LAI[c] (E)	CANOPY COVER[c] (F)	FULLSTAND-EDNESS[d] (G)	SUMMED RANK (A+C+F)	SUMMED RANK (ALL VARIABLES)
CONTROL	75.8 (5)	78.7 (2)	88.7 (4)	105.3 (2)	75.6 (2)	62.5 (3)	33.0 (1)	4	2
FERTILIZED	62.0 (1)	65.5 (1)	86.3 (2)	73.7 (1)	77.8 (3)	40.7 (1)	40.0 (3)	1	1
PESTICIDE	72.0 (4)	-- --	90.6 (5)	-- --	69.2 (1)	58.5 (2)	47.0 (5)	5	--
DEFOLIATED	66.4 (3)	-- --	74.7 (1)	-- --	-- --	-- --	41.4 (4)	3	--
WATERED	63.3 (2)	-- --	86.7 (3)	-- --	-- --	-- --	34.0 (2)	2	--

[a] at final harvest
[b] at flowering
[c] second LAI/canopy cover sample
[d] third stand count

in Year 2 may have been due to the greater amount of residual leaf area left after defoliation. No strong evidence was found to support the idea that intercropping systems are more resilient following defoliation than are corresponding monocultures. In Year 1 the maize-cowpea system was more resilient after defoliation than corresponding monocultures, but resilience of other intercrops was about the same as (or lower than) that of corresponding monocultures. In both years the four-crop system did not recover as completely as corresponding monocultures.

Pesticide spraying increased cowpea yields, slightly increased LAI in the four-crop system, and was phytotoxic to pumpkin. Stability of the four-crop system with respect to both the pesticide and watering treatments was approximately equal to that of corresponding monocultures.

Stability at different intensities of stress

A nutrient rich (low nutrient stress) environment increased stability of all systems taken as a whole (Table 50). Variability among plots of all systems was consistently lower in fertilized plots than in controls. No clear differences in system stability were evident for the other stress treatments. Reduced coefficients of variation in the fertilized treatment were due not only to higher mean yield, but also to reduced absolute variation in productivity.

Stability with respect to competition

The increased risk of crop failure associated with high density monocultures (especially maize, Dowker 1963) is an important issue for third world agricultural development, as is the potential for intercropping systems to respond positively to increased planting density

without increased risk of crop failure. Response of system productivity and stability to packing (overall density, or level of competition within the system as a whole) were not tested for in this study, but the performance of the sparse and normal density maize monocultures was interesting in this regard. Maize monoculture at recommended density (44,000 plants/ha) was less stable with respect to defoliation than the sparse density stand (22,000 plants/ha). Variability among plots (Year 1 only) was lower in the dense system in the small control and defoliated plots, but the sparsely-planted system was more stable in the larger main-experiment control plots. The edible and total yield of the sparse monoculture exceeded that of the dense monoculture, significantly in the case of edible yield. These results strongly support the idea of reduced productivity in dense monoculture plantings, but are not conclusive regarding the effects of planting density on monoculture stability.

Summary

Findings regarding stability of system productivity are summarized in Table 51. Responses to the defoliation, pesticide, and watering treatments are omitted because of nonsignificance. The sorghum and four-crop systems were the most stable (constant) in terms of year-to-year fluctuation, among-plot variability in Years 1 and 2, and responses to fertilization. Successional vegetation was also relatively stable, while maize, cowpea, and pumpkin monocultures were unstable. The four-crop was consistently more stable than corresponding monocultures.

Table 51. Summary of ranking of systems by several measures of stability. 1=lowest coefficient of variation or percent change (most stable). Performance of corresponding monocultures is also given where possible. In the experimental design of this study the monoculture plots were not paired, so point-to-point (plot-to-plot) variation of a weighted sum of monocultures could not be calculated.

SYSTEM	YEAR-TO-YEAR FLUCTUATION[a]	FLUCTUATION AMONG PLOTS, YEAR 1[b]		FLUCTUATION AMONG PLOTS, YEAR 2[c]	BIOMASS RESPONSE TO FERTILIZATION[d]	LAI RESPONSE TO FERBILIZATION[d]	SUMMED RANK
MAIZE	2.5	6.5	(5)	4	6	5	22.5
SPARSE MAIZE	--	9		--	--	--	
SORGHUM	1	1	(1)	1	1	2	6
COWPEA	6	4	(3)	5	3	7	24
PUMPKIN	7	10	(6)	6	7	1	27
MAIZE-SORGHUM	--	3		--	--	--	
MAIZE-COWPEA	--	8		--	--	--	
MAIZE-PUMPKIN	--	6.5		--	--	--	
FOUR-CROP	4	2	(2)	2	2	3	13
CORRESPONDING MONOCULTURES	5	--		--	4	4	
SUCCESSION	2.5	5	(4)	3	5	6	20.5

[a]coefficient of variation of total biomass, LAI, and canopy cover, control plots (summed rank)

[b]coefficient of variation of total biomass, control and defoliated plots (rank). Values in parentheses are ranks of Year 2 systems only, and were used for the summed rank calculation.

[c]coefficient of variation of total biomass, root and shoot biomass at flowering, LAI, and canopy cover, all treatments combined (summed rank).

[d]fertilization increase as percent of control (rank)

Species Stability

To determine whether each species was more stable in the four-crop intercrop or in monoculture, the same analyses were performed as for system stability, but on variables that measured each species' productivity, adjusted for planting density in the intercrops.

Year-to-year fluctuations

Year-to-year fluctuations in total biomass, edible biomass, and LAI (Table 52) were greatest for pumpkin and cowpea, intermediate for successional monocots and dicots, and low for maize and sorghum. Maize and sorghum edible and total biomass tended to vary less from year to year than LAI; biomass of cowpea, pumpkin, successional monocots, and successional dicots varied more than LAI. When the intercrop and monoculture stabilities for each of the three variables were ranked and the ranks summed, the index of stability obtained was higher in monocultures for each of the four crop species. The lower stability in intercrop was especially evident for cowpea and pumpkin; the difference was much lower in sorghum, and almost negligible in maize.

Plot-to-plot variability within years

Analysis of variation among plots in Years 1 and 2 (all treatments combined) gave results closely matching those from the year-to-year comparison (Tables 53 and 54). Yield fluctuations were consistently lower in monoculture than in the intercrop systems. The only exception was Year 2 maize, which was more stable in the four-crop system than in monoculture by all measures except fullstandedness.

Table 52. Year-to-year yield stability of each species. Values are coefficients of variation between Year 1 and Year 2 control plot means of edible biomass, total aboveground biomass, and LAI.

		COEFFICIENT OF VARIATION		
SPECIES	SYSTEM	BIOMASS[a]	EDIBLE BIOMASS[a]	LAI[b]
MAIZE	MONOCULTURE	.01	.03	.28
	FOUR-CROP	.04	.06	.21
SORGHUM	MONOCULTURE	.03	0	.13
	FOUR-CROP	.27	.02	.38
COWPEA	MONOCULTURE	.45	.55	.31
	FOUR-CROP	.98	1.22	.81
PUMPKIN	MONOCULTURE	.51	1.41	.44
	FOUR-CROP	1.29	--	1.22
MONOCOTS	SUCCESSION	.37	--	.34
DICOTS	SUCCESSION	.61	--	.20

[a]at harvest

[b]second LAI sample in Year 2 (day 65); Year 1 LAI linearly interpolated to day 65

Table 53. Yield stability of each species in intercrops and monoculture, Year 1. Values are coefficients of variation of edible and total aboveground biomass among plots (n = 6, a sample of control and defoliation plots combined).

SPECIES	SYSTEM	COEFFICIENT OF VARIATION EDIBLE BIOMASS	TOTAL BIOMASS
MAIZE	MAIZE	28.2	25.2
	SPARSE MAIZE	32.6	36.4
	MAIZE-SORGHUM	48.2	35.6
	MAIZE-COWPEA	40.9	29.4
	MAIZE-PUMPKIN	20.8	45.4
	FOUR-CROP	30.9	16.9
SORGHUM	SORGHUM	15.6	17.3
	MAIZE-SORGHUM	14.2	17.3
	FOUR-CROP	47.5	39.7
COWPEA	COWPEA	32.2	20.3
	MAIZE-COWPEA	51.8	39.3
	FOUR-CROP	30.4	31.7
PUMPKIN	PUMPKIN	--	25.2
	MAIZE-PUMPKIN	--	86.8
	FOUR-CROP	--	42.3
MONOCOTS	SUCCESSION	--	22.9
DICOTS	SUCCESSION	--	47.3

Table 54. Yield stability of each crop species in intercrop and monoculture, Year 2. Values are coefficients of variation of the variables listed vertically. n = 11-25, a sample of all treatments combined. Asterisks indicate the more constant system.

SPECIES VARIABLE	MONOCULTURE	FOUR-CROP
MAIZE		
BIOMASS[a]	62.9	58.3*
BIOMASS[b]	59.0	46.3*
EDIBLE BIOMASS[a]	85.8	73.4*
ROOTS[d]	69.0	62.3*
LAI[c]	65.6	45.9*
FULLSTANDEDNESS[d]	12.8*	23.8
SORGHUM		
BIOMASS[a]	38.5	36.3*
BIOMASS[b]	47.0	40.6*
EDIBLE BIOMASS[a]	43.5*	52.1
ROOTS[b]	52.3*	54.5
LAI[c]	35.5*	45.5
FULLSTANDEDNESS[d]	12.8*	16.3
COWPEA		
BIOMASS[a]	72.0	71.5*
BIOMASS[b]	143.2	95.6*
EDIBLE BIOMASS[a]	112.8*	133.3
ROOTS[b]	82.5	72.6*
LAI[c]	81.3	55.5*
FULLSTANDEDNESS[d]	13.7*	15.7
PUMPKIN		
BIOMASS[a]	136.8*	181.4
BIOMASS[b]	115.0*	227.8
EDIBLE BIOMASS[a]	171.2	--
ROOTS[b]	105.1*	147.6
LAI[c]	141.8*	165.6
FULLSTANDEDNESS[d]	77.6*	109.8

[a] at harvest

[b] at flowering

[c] second LAI sample

[d] third stand count

Responsiveness to the stress treatments

Species response and responsiveness to the stress treatments are shown in Tables 55 and 56. Defoliation significantly reduced sorghum yield in the Year 1 four-crop system but did not significantly affect yields of other species. Pumpkin responded more positively to defoliation in intercrop than monoculture in both years. Although the difference was not significant, this trend strongly suggests that increased light penetration in the defoliated four-crop system stimulated compensatory growth in pumpkin, whereas factors other than light were limiting to the pumpkin monoculture. Dicots also responded much more positively to defoliation than their monocot neighbors, as expected from the low position of dicot leaves in the canopy. The method used to remove leaf area (clipping to 15 or 20 cm) resulted in greater leaf removal from monocots than dicots. Nevertheless, the consistent positive response of successional dicots and intercropped pumpkin to defoliation was very likely to be a compensatory growth response to increased light levels.

Maize also responded more positively to defoliation in the intercrop systems than in monocultures in Year 1, but the opposite was true in Year 2. (None of the differences from controls was significant.) Sorghum consistently responded negatively to defoliation (significantly), and responded even more negatively in the four-crop and maize-sorghum intercrop than in monoculture. The fact that defoliation took place relatively late in the life cycle of sorghum may explain its low capacity to recover. Greater competitiveness of maize than sorghum following defoliation may be responsible for the even slower recovery

Table 55. Stability of each species with respect to defoliation, Year 1. Effects of defoliation on total aboveground biomass are expressed as both absolute change and percent of control. Asterisk indicates significant differences from control.

		EFFECT OF DEFOLIATION ON TOTAL ABOVEGROUND BIOMASS, COMPARED WITH CONTROL	
SPECIES	SYSTEM	g/m^2	% CONTROL
MAIZE	SPARSE MAIZE	-38	-10
	MAIZE	-45	-22
	MAIZE-SORGHUM	42	21
	MAIZE-COWPEA	80	21
	MAIZE-PUMPKIN	-284	-56
	FOUR-CROP	27	7
SORGHUM	SORGHUM	-28	-11
	MAIZE-SORGHUM	-64	-22
	FOUR-CROP	-198	-49*
COWPEA	COWPEA	-.4	-5
	MAIZE-COWPEA	2	23
	FOUR-CROP	-6	-38
PUMPKIN	PUMPKIN	-11	-8
	MAIZE-PUMPKIN	21	71
	FOUR-CROP	8	22
MONOCOTS	SUCCESSION	-4	-3
DICOTS	SUCCESSION	7	49

Table 56. Stability of each species with respect to fertilization, spraying, defoliation, and watering, Year 2. Effects of the treatment are given as both absolute change and percent of control.

TREATMENT EFFECT ON TOTAL ABOVEGROUND BIOMASS, COMPARED WITH CONTROL

		FERTILIZED		PESTICIDE		DEFOLIATED		WATERED	
SPECIES	SYSTEM	g/m^2	%	g/m^2	%	g/m^2	%	g/m^2	%
MAIZE	MONOCULTURE	435	178†	1	0	53	22	2	1
	FOUR-CROP	565	109†	-188	-36	-175	-34	-87	-17
SORGHUM	MONOCULTURE	201	57‡	3	1	-40	-11‡	-106	-30
	FOUR-CROP	170	31	-58	-11	-218	-40	-74	-14
COWPEA	MONOCULTURE	20	102	91	466†	46	234	35	178
	FOUR-CROP	33	48	105	154†	-21	234	24	-35
PUMPKIN	MONOCULTURE	3	150	-2	-90	-2	-90	-1	-32
	FOUR-CROP	127	243†	-45	-87	12	24	-28	-53
MONOCOTS	SUCCESSION	336	203†	84	51	7	4	39	24
DICOTS	SUCCESSION	-11	-10	36	34	80	76	-28	-26

TREATMENT EFFECT ON LAI, COMPARED WITH CONTROL

		FERTILIZED		PESTICIDE	
SPECIES	SYSTEM	AMOUNT	%	AMOUNT	%
MAIZE	MONOCULTURE	.60	110‡	-.17	-31
	FOUR-CROP	.41	47	-.24	-27
SORGHUM	MONOCULTURE	.38	52†	.04	6
	FOUR-CROP	.82	126	.24	36
COWPEA	MONOCULTURE	.92	345‡	1.36	508‡
	FOUR-CROP	.24	26	1.07	114
PUMPKIN	MONOCULTURE	.06	14	-.33	-85
	FOUR-CROP	.07	224	-.03	-100
MONOCOTS	SUCCESSION	1.20	195†	.01	2
DICOTS	SUCCESSION	.28	36	-.12	-16

†significant treatment effect compared with controls (Duncan's test)

‡significant treatment effect compared with controls (Duncan's test on a sample of the four-crop and monoculture systems combined)

of sorghum in intercrop than monoculture. Cowpea responded positively to defoliation in Year 2 (nonsignificantly) but not in Year 1; no clear differences in its response in intercrop and monoculture were found.

The Year 2 watering treatment had no significant effect on any species' productivity. Pesticide spraying significantly increased cowpea yield. Cowpea responsiveness to spraying was higher in monoculture than in the four-crop system, indicating that the intercrop was more stable with respect to fluctuating pest levels.

Fertilization produced significant increases in biomass and/or LAI in all agronomic species and successional monocots (but not successional dicots). Maize and cowpea responsiveness was higher in the four-crop intercrop than in monoculture; sorghum LAI responsiveness was higher in intercrop, but biomass responsiveness was higher in monoculture. Pumpkin was consistently more responsive to fertilization (less stable) in intercrop than in monoculture.

Summary of species stability in intercrops and monocultures

Species stability in intercrop and monocultures by the above analyses are summarized in Table 57. Sorghum, cowpea, and pumpkin tended to be more stable in monocultures, whereas maize was more stable in the intercrop system.

Stability with respect to competition

The responsiveness of the crop species to a change from intra- to interspecific competition (at the same overall functional density) was

Table 57. Summary of ranking of systems by each species' yield stability. 1 = lowest coefficient of variation or percent change from control (most stable).

SPECIES	SYSTEM	YEAR-TO-YEAR FLUCTUATIONS[a]	FLUCTUATION AMONG PLOTS, YEAR 1[b]	FLUCTUATION AMONG PLOTS, YEAR 2[c]	BIOMASS RESPONSE TO FERTILIZATION[d]	LAI RESPONSE TO FERTILIZATION[d]	SUMMED RANK
MAIZE	MAIZE	1.5	1.5 (1.5)	2	2	2	9
	SPARSE MAIZE		5				
	MAIZE-SORGHUM		6				
	MAIZE-COWPEA		4				
	MAIZE-PUMPKIN		3				
	FOUR-CROP	1.5	1.5 (1.5)	1	1	1	6
SORGHUM	SORGHUM	1	1.5 (1)	1.5	2	1	6.5
	MAIZE-SORGHUM		1.5				
	FOUR-CROP	2	3 (2)	1.5	1	2	8.5
COWPEA	COWPEA	1	1 (1)	1	2	2	7
	MAIZE-COWPEA		3				
	FOUR-CROP	2	2 (2)	2	1	2	9
PUMPKIN	PUMPKIN	1	1 (1)	1	1	1	5
	MAIZE-PUMPKIN		3				
	FOUR-CROP	2	2 (2)	2	2	2	10

[a]coefficient of variation of edible biomass, total biomass, and LAI in control plots (summed rank). Systems were ranked equally when rankings of the three measures were inconsistent.

[b]coefficient of variation of edible and total biomass in control and defoliated plots (summed rank). Systems were ranked equally when rankings of the two variables were inconsistent. Values in parentheses are ranks of Year 2 systems only, which were used for the calculation of the summed rank (last column).

[c]coefficient of variation of edible biomass, total biomass, root and aboveground biomass at flowering, and LAI (summed rank). Systems were ranked equally when the ranking of more than one variable was inconsistent with the rest.

[d]fertilization increase as percent of control (ranked).

evaluated by expressing the difference in each species' yield in intercrop and monoculture as percent of monoculture yield (Table 58). Maize was highly responsive to changes in neighbors. Maize edible yield responded even more strongly than total yield, reflecting increased allocation ratios, number of cobs, and edible yield per cob in the intercrop system. Cowpea was also highly responsive to the switch from intra- to interspecific competition, especially in Year 2, when pests and diseases seemed to be less limiting (see Chapter Five). Cowpea edible yield, like maize edible yield, responded even more positively to reduced competition than did total biomass. Sorghum was much more stable with respect to competition than either maize or cowpea. Pumpkin responded strongly, but negatively, to substitution of maize, sorghum, and cowpea neighbors for other pumpkin plants.

Discussion: Sources of System Stability

An Artifact of Coefficient of Variation Calculations?

One could argue that the lower coefficients of variation found in diverse systems are merely artifacts of division by the mean in the calculation of the coefficients; since productivity was higher in the intercrop systems, lower coefficients of variation would seem to follow automatically.

The validity of the coefficient of variation as a measure of stability has a biological basis. Functional responses are as a rule proportional to the amount of structure present, causing standard deviations of productivity measures to vary with the mean. Reduced

Table 58. Stability of each species with respect to competition. Effects of intercropping are given as both absolute changes from monoculture yield and percent change from monoculture. Edible and total biomass are adjusted for planting density in the intercrop.

		EFFECTS OF INTERCROPPING, COMPARED WITH MONOCULTURE			
		TOTAL BIOMASS		EDIBLE BIOMASS	
SPECIES	YEAR	g/m^2	%	g/m^2	%
MAIZE	1	236	94	120	188
	2	274	113	117	221
SORGHUM	1	33	10	-1	0
	2	193	55	37	73
COWPEA	1	3	30	0	13
	2	50	263	9	569
PUMPKIN	1	-57	-58	--	--
	2	-50	-06	-25	-100

coefficient of variation implies reduced response relative to the biomass present, a quality distinct from the absolute magnitude of the response. The magnitude of response relates to resource use, whereas response per unit biomass (my "responsiveness") relates to the elusive quality called stability, the ability to maintain constant productivity under varying types and intensities of stressors.

Responsiveness (response per unit biomass) is intriguingly similar to the ratio of productivity to biomass, which Margalef (1969) shows mathematically to be inversely related to (his measure of) stability and directly related to (his measure of) diversity, and which van Emden and Williams (1974) conclude is the best measure of system stability. Response of a species or system per unit biomass is a property of interest in its own right, then, regardless of whether its value is more influenced by changes in the magnitude of fluctuations or by changes in the amount of standing structure.

Masking of Species' Fluctuations

Fluctuations in a given species may be masked (as opposed to being buffered) due simply to the presence of other species in the system that contribute biomass but do not respond at the same time or to the same degree to environmental changes. When several different species response curves (or surfaces, or volumes, if more than one limiting factor is being considered) are added up into a system response curve, the fluctuations of each species (as percent system biomass) are damped by a simple dilution effect. This system characteristic explains why the stability of the four-crop system fell between that of its most stable

member (sorghum) and its least stable member (pumpkin). The more even the distribution of biomass among species, the greater the average masking of species fluctuations. The greater the proportion of biomass a species contributes, the more its responses will influence system responses.

Buffering of Species' Fluctuations

Species' fluctuations may be buffered by compensatory growth, reducing system responsivenes. Resource partitioning, on the other hand, would not seem to imply greater system stability, except to the extent that it allows compensatory growth. The higher productivity of the intercrop systems, and the negative correlation of cowpea growth with growth of maize and pumpkin (on a plot-to-plot basis) strongly suggest that compensatory growth was one mechanism operating to increase stability of the intercrop systems. Compensation was not, however, directly tested for with plant-removal experiments.

Increased Stability of Component Species

Increased stability of one or more components of a diverse system could be the cause of greater stability of the system as a whole, rather than differences in species interactions (masking and buffering effects). In the results of this study, the slight increase in maize stability in the intercrop systems could counteract the decreased stability of the other three species. Increased maize stability in intercrop was almost certainly responsible for the increased stability of the maize-cowpea and maize-pumpkin intercrops, where maize contributed more than 80 percent of system biomass. It seems unlikely, however, that increased

maize stability alone could explain the increased system stability of the maize-sorghum and four-crop systems compared with their corresponding monocultures.

Alternatively, the reduced stability of sorghum, cowpea, and pumpkin in intercrop could contribute positively to stability of the system as a whole through compensatory growth. If compensatory growth occurs in intercrop systems, it could account for the tendency of yields of responsive species to fluctuate more in intercrops than they do in monoculture. In monoculture a crop experiences a uniform competitive enviornment over time, space, and stress intensities, but in the intercrop system the competitive environment is likely to fluctuate due to differing responses of neighboring species to environmental fluctuations. Each species' compensatory response to the variable competitive environment would appear as species instability, but would contribute to the stability of the system as a whole.

High responsiveness of individual species to change in competition implies high capacity for compensatory growth. The high responsiveness of maize yield (especially edible yield) to changes in competition are a good reason to include it in intercrop systems. Cowpea and pumpkin were also highly responsive to changes in competition. Pumpkin responded negatively to substitution of unlike for like neighbors, presumably due to increased competition for light, but this responsiveness nevertheless implies a capacity for compensatory growth. Sorghum, in contrast, did not respond dramatically to changes in competition. Although the physiological basis of sorghum yield stability is not known, this study has demonstrated that while sorghum does have some capacity

for compensatory growth, its yield remains stable over a range of environmental conditions. Other researchers (Doggett and Jowett 1966, Rao and Willey 1980) also found sorghum to have high yield stability.

The lower year-to-year fluctuation of maize and sorghum compared with cowpea and pumpkin may reflect greater environmental instability in terms of pests and diseases than in terms of growth factors such as light, water, and nutrients. Rainfall was good in both study years, an unusual circumstance not characteristic of the unpredictable rainfall regime. Pest levels of cowpea and pumpkin varied widely from year to year, while those of maize and sorghum were more constant (see Chapter Five).

Stress Intensity and Stability

Species or systems are expected to be more stable under low stress than high stress if the Michaelis-Menton equation is used to represent the productivity response to limiting factors. Mitsch (1975) reviews alternative models for limiting-factor responses, some of which are straight-line responses up to a threshold. Straight-line models, unlike the Michaelis-Menton model, would give equal stability (responsiveness) up to the threshold.

Using the Michaelis-Menton equation as a starting point, one can derive expressions for response (change in productivity with change in a factor) and responsiveness (response as a fraction of biomass). These expressions, and examples of graphs of the functions when all constants are set to one, are shown in Figure 84. Both response and responsiveness are greater at lower factor levels (higher stress); at

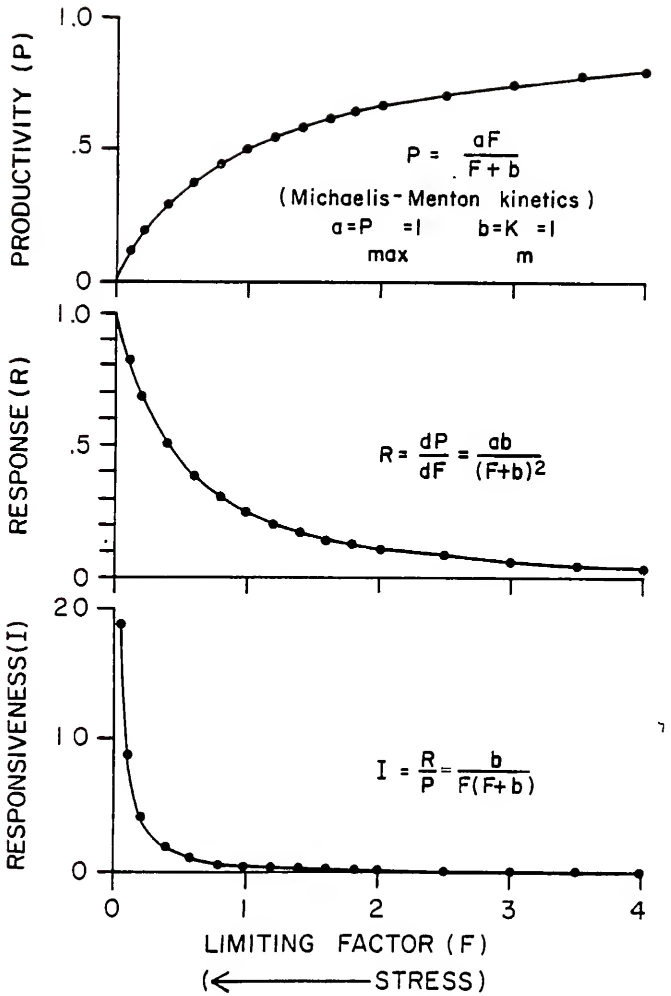

Figure 84. Productivity, response, and responsiveness (instability) as functions of one limiting factor. Curves are based on hypothetical values of 1 for P_{max} and K_m.

higher factor levels (lower stress), both are reduced. The shape of the response and responsiveness curves are not identical, due to differences in productivity at varying intensities of stress. At intermediate stress, stability may be very high despite rather large changes in productivity (response). At very high stress, instability can be extremely high, while the absolute response reaches a finite maximum.

The finding of greater system productivity and stability in the fertilized treatment than in controls is consistent with these relationships. It is difficult to quantitatively assess the relationship, however, because no measure of stress was obtained independent of productivity; when several kinds of stressors are being compared, measures related to productivity are some of the few quantitative measures of stress available.

Interaction Among Stressors

Stressors may or may not interact before (or while) impinging on species or system productivity, but they do interact through the productivity response of the system/organism being impacted. Limiting factors are generally recognized as being multiplicative in their effects on productivity (Mitsch 1975, Odum 1971). The effects of factor interaction on the response and responsiveness functions are less clear.

The interaction of competition and fertilization is not an ideal example of interacting factors, however, since the two factors may be strongly interrelated through soil nutrient levels. If this is a case of two ways of altering soil nutrient availability, rather than two

independent interacting factors, the expected results are quite different. At higher levels of nutrients (for whichever reason), response and responsiveness to additional change in nutrients should be reduced (equivalent to moving the bottom two graphs in Figure 84 to the left). In real ecosystems, it is likely that such direct interactive effects are extremely common and would result in greater stability to additional stressors in initially unstressed systems.

In Table 59, expressions are derived for productivity, response, and responsiveness as a function of two factors that interact as Michaelis-Menton functions. For simplicity, the expressions are given as functions of the first limiting factor, x, at two finite levels (z_1 and z_2) of the second factor, z. Levels of the factor z influence productivity and response with respect to factor x. The second factor may either increase or decrease response to the first, depending on its level and the values of the constants a,b,c, and d. The factor z and its constants are absent from the expressions for responsiveness, however, showing that interaction with factor z does not influence responsiveness with respect to factor x. Based on this model, productivity and productivity response are multiplicative functions of two interacting stressors; stability is an additive function.

Intercrop and monoculture response and responsiveness to the stress treatments can be viewed as an example of factor interaction. The first factor is intensity of competition among species in the system; the second factor is the stress treatment. By the Michaelis-Menton model, the productivity advantage of intercropping should be even greater in fertilized than control plots, but the stability advantage of the diverse system should be independent of the intensity of other stressors.

Table 59. Productivity, response, and responsiveness as functions of two interacting limiting factors. Expressions for productivity (P), productivity response (R), and responsiveness (I, instability) are given at two levels (z_1 and z_2) of factor z, expressed in terms of a second factor x; a, b, c, and d are Michaelis-Menton constants.

	CONDITION $z = z_1$	CONDITION $z = z_2$
PRODUCTIVITY (P)	$\frac{ax}{(x+b)} \cdot \frac{cz_1}{(z_1+d)}$	$\frac{ax}{(x+b)} \cdot \frac{cz_2}{(z_2+d)}$
RESPONSE (R) $= \frac{dP}{dx}$	$\frac{abcz_1}{(z_1+d)} \cdot \frac{1}{(x+b)^2}$	$\frac{abcz_2}{(z_2+d)} \cdot \frac{1}{(x+b)^2}$
RESPONSIVENESS (I) $= \frac{R}{P}$	$\frac{b}{x(x+b)}$	$\frac{b}{x(x+b)}$

Only the interaction between fertilization and competition will be discussed here since the other treatments did not have significant effects on productivity. Although the response to fertilization was equal in the four-crop system and corresponding monocultures, the responsiveness of both biomass and LAI was higher in the monoculture system. The response to changes in competition (intercrop minus monoculture yield) was also approximately equal, about 110 g/m^2, in the control and fertilized plots. Responsiveness to changes in competition (response/ monoculture yield), however, was considerably higher in the control than the fertilized treatment (70 and 31 percent increase, respectively). These results suggest that effects of two interacting factors upon stability as well as productivity are nonadditive.

CHAPTER FIVE
PESTS, DISEASES, AND OTHER NATURAL STRESSORS

In this chapter, effects of intercropping and effects of the stress treatments on levels of various pests, diseases, and other naturally-occurring stressors are analyzed. Degree to which pests influence crop productivity is examined using correlation analysis. Stability of pest populations between years, among plots, and among the stress treatments are evaluated. Implications of the results are discussed.

Results

Weed Biomass

In both study years, significant differences in weed biomass among systems were found only in the third weeding (growth from day 39-78 in Year 1, day 44-107 in Year 2); data from the other weedings are included in Figures 85-88 but are not discussed. In Year 1 (Figure 85), weed growth was significantly greater in the bare ground and cowpea systems than all other agronomic systems (of which pumpkin monoculture had the next highest weed growth). In Year 2 (Figure 86), there was significantly greater weed growth in cowpea and pumpkin monocultures than in the maize, sorghum, and four-crop systems. In Year 2, fertilization increased weed biomass slightly in the pumpkin, cowpea, and maize systems, and increased weeds substantially in the four-crop and sorghum systems (Figure 87). Watering increased weed growth even more than fertilization in the pumpkin, cowpea, and four-crop systems;

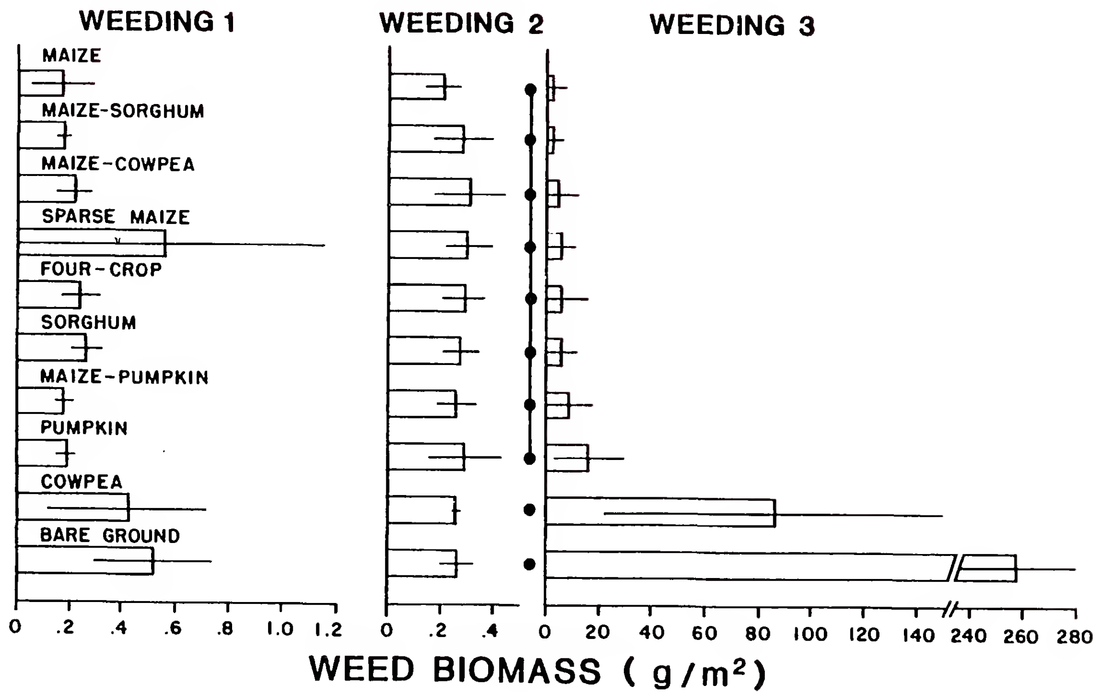

Figure 85. Weed biomass by system at three weeding times, Year 1. Duncan's tests gave no significant differences among systems in weeding 1 (day 0-17 growth) or weeding 2 (day 17-39 growth). In weeding 3 (day 39-78 growth), systems not connected by a vertical line are significantly different by Duncan's tests.

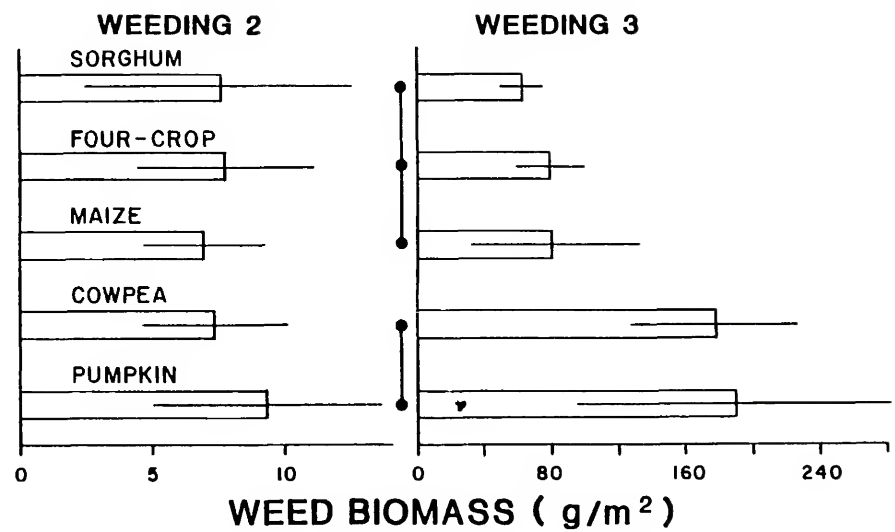

Figure 86. Weed biomass at two weeding times in the control treatment, Year 2. No significant differences among systems were found in weeding 2 (day 24-44 growth) by Duncan's test, performed on a sample of all treatments combined (not shown in the growth); systems not connected by a vertical line in weeding 3 (day 44-107 growth) are significantly different by the same kind of Duncan's test.

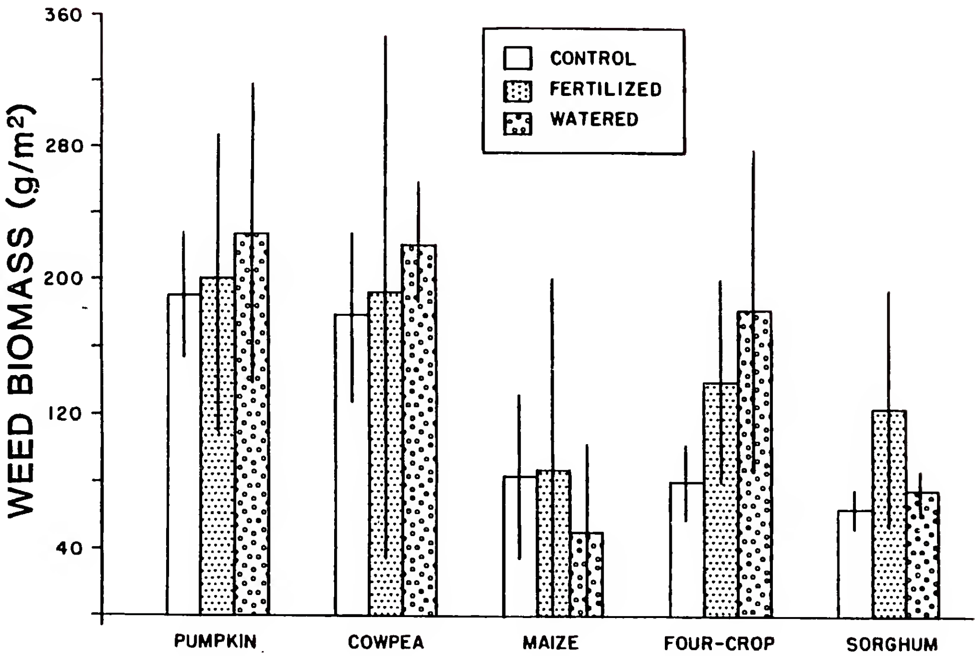

Figure 87. Weed biomass in three treatments, Year 2. Data are from weeding 3, (growth from day 44-107). No significant differences among treatments were found by Duncan's test, performed on a sample of all systems combined.

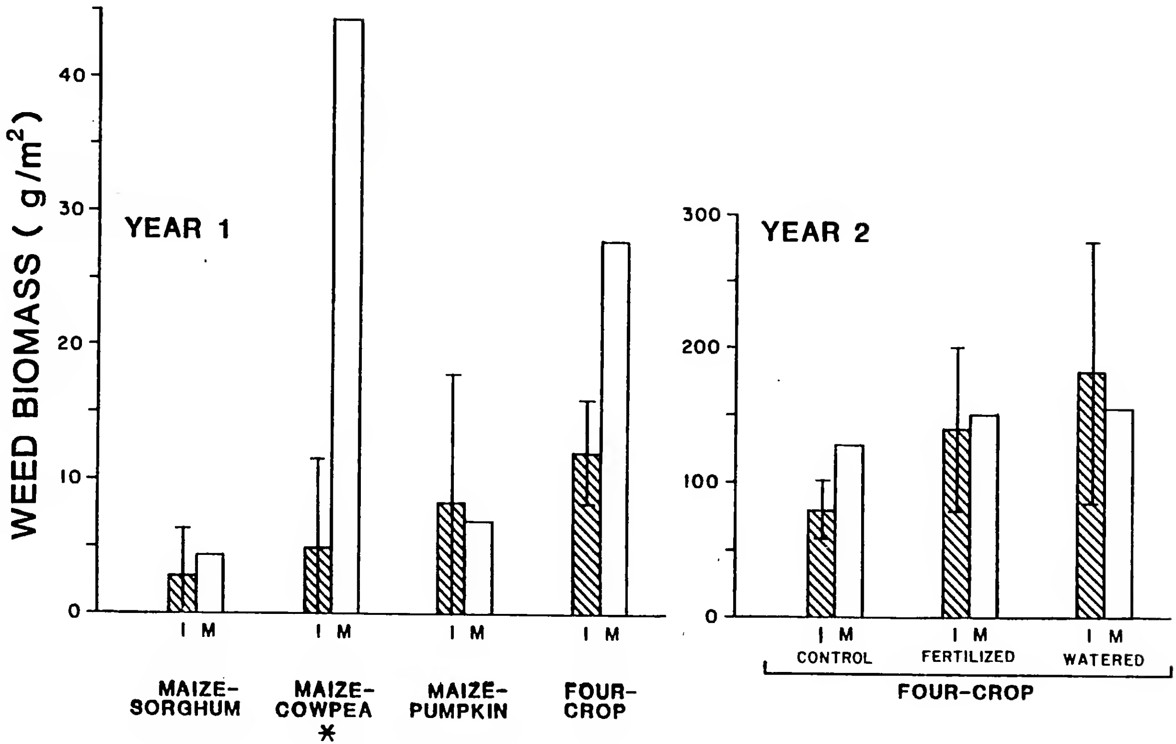

Figure 88. Comparison of weed biomass in intercrops and corresponding monocultures, Years 1 and 2. Data are from weeding 3 (day 39-78 growth in Year 1; day 44-107 growth in Year 2). I = intercrop (hatched bars); M = corresponding monocultures. Significant intercrop/monoculture differences (by SAS Contrast procedure) are indicated with an asterisk. No significant intercrop/monoculture differences were found at other weeding times.

increased weeds slightly in the sorghum system (compared with controls); and decreased weed growth in the maize system. None of these treatment differences were significant, however.

Weed biomass was significantly lower in the maize-cowpea intercrop system than in corresponding monocultures in Year 1, and substantially lower in the four-crop system than in corresponding monocultures in both study years (Figure 88). Weed growth was approximately equal in intercrops and corresponding monocultures in the maize-sorghum and maize-pumpkin intercrops in Year 1, and in the fertilized and watered four-crop system in Year 2.

Maize and Sorghum Lodging

Percent of maize plants lodged after windstorms was higher than percent lodged sorghum plants in both years (Figure 89). Rates of lodging of both species did not vary significantly among the cropping systems, although maize lodging in the four-crop system was less than half that in the maize monoculture in both years. Sorghum lodged slightly more in the four-crop system than in monoculture in both years. Maize lodging was slightly lower (sorghum lodging slightly higher) in defoliated than control plots in Year 2; the differences were not significant.

Striga

Populations of maize and sorghum parasites of the genus *Striga* were highly variable from plot to plot, and did not vary significantly among systems in Year 1 main plots or small control plots (Figure 90).

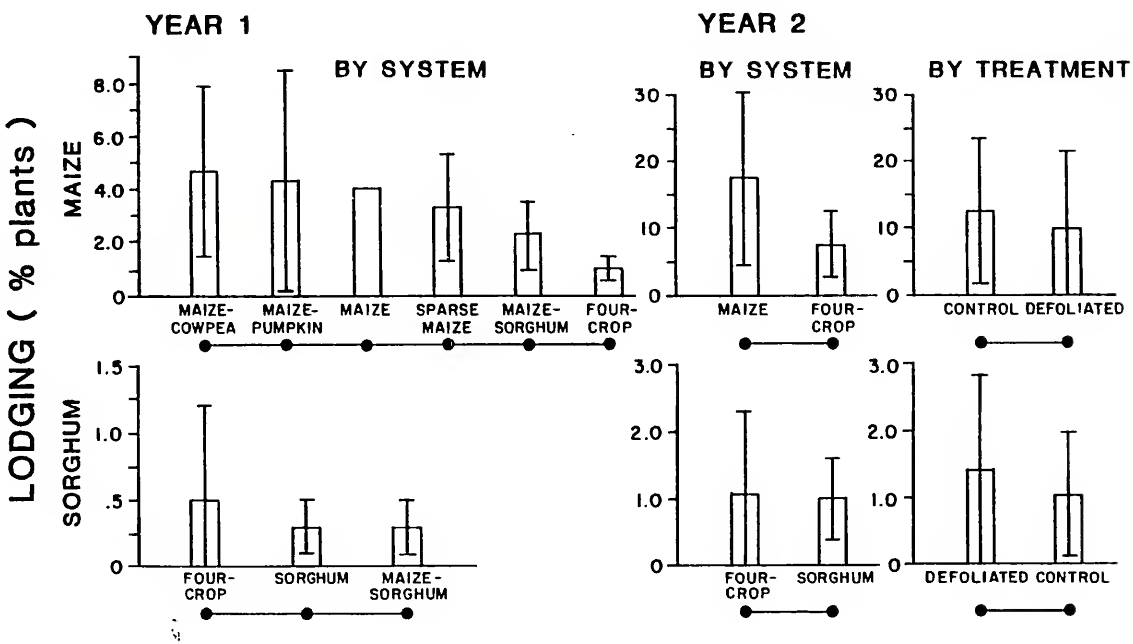

Figure 89. Maize and sorghum lodging, Years 1 and 2. Histograms of system differences are based on the control treatment; histograms of treatment differences include all systems. Systems or treatments not connected by a common line are significantly different by Duncan's tests, performed on samples of all systems or treatments combined.

EXPERIMENT	SYSTEM DIFFERENCES						
YEAR 1 MAIN PLOTS	MAIZE-PUMPKIN 134.5	MAIZE-SORGHUM 27.6	FOUR-CROP 23.8	MAIZE-COWPEA 17.6	SPARSE MAIZE 16.0	MAIZE 12.4	SORGHUM 4.2
YEAR 1 SMALL PLOTS	MAIZE 52.8	MAIZE-SORGHUM 22.2	SPARSE MAIZE 15.3	MAIZE-PUMPKIN 12.5	FOUR-CROP 8.3	MAIZE-COWPEA 0	

Figure 90. Striga populations, Year 1. Data are no. individuals/100 m^2, and are from control plots only. Sorghum monoculture was not monitored in the small plots. Systems sharing a common line are not significantly different by Duncan's tests.

Rats

The density of rat holes after planting did not vary significantly among systems in Year 1 (Figure 91). Maize and cowpea appeared to be the preferred seeds, however; pumpkin and cowpea monocultures (and the maize-pumpkin and maize-cowpea intercrops) had no seed herbivory by rats.

Maize Pests and Diseases

Maize streak symptoms appeared in 12-16 percent of the maize populations in Years 1 and 2; differences among systems were nonsignificant in both years (Figure 92). In Year 2, streak levels were lowest in the pesticide treatment and highest in the watered plots, but none of the treatments differed significantly from controls.

"Windowing" in leaves from maize stalk borers (day 13, Year 1) was slightly more frequent in the four-crop system than in maize monoculture (9.1 and 8.0 percent of plants, respectively) (Figure 92). No significant differences in stalk borer levels were found among the control, fertilization, and watering treatments, although the highest levels were found in fertilized plots. (Defoliation and pesticide treatments were not effective at the time of the sample.)

Sorghum Pests and Diseases

Sorghum shootfly damage (Figure 93) was greater in the four-crop system than in sorghum monoculture in both study years; the difference was significant only in Year 2. Pesticide-treated plots had significantly lower percent of plants with "dead heart" than all other treatments.

MAIZE-COWPEA	SPARSE MAIZE	FOUR-CROP	MAIZE	COWPEA	MAIZE-PUMPKIN	MAIZE-SORGHUM	PUMPKIN	SORGHUM
4.7	3.5	1.5	1.2	.2	0	0	0	0

Figure 91. Seed consumption by rats, Year 1. Data are no. rat holes/80 m^2 plot, and are from all the Year 1 small plots. Systems sharing a common line are not significantly different by Duncan's test.

PARAMETER	SYSTEM AND TREATMENT DIFFERENCES					
MAIZE STREAK (YEAR 1)	MAIZE-PUMPKIN 16.4	FOUR-CROP 15.3	MAIZE 14.4	MAIZE-SORGHUM 13.3	MAIZE-COWPEA 12.4	SPARSE MAIZE 12.2
MAIZE STREAK (YEAR 2)	MAIZE 16.7	FOUR-CROP 14.5				
	WATERED 21.1	DEFOLIATED 17.1	CONTROL 16.8	FERTILIZED 14.1	PESTICIDE 10.2	
MAIZE STALK BORER (YEAR 2)	FOUR-CROP 9.1	MAIZE 8.0				
	FERTILIZED 9.4	CONTROL 7.9	WATERED 4.9			

Figure 92. Maize streak and maize stalk borer frequencies, Years 1 and 2. Data are percent of plants with symptoms. Systems or treatments not sharing a common line are significantly different by Duncan's tests, performed on a sample of all systems or treatments combined.

PEST	SYSTEM DIFFERENCES			TREATMENT DIFFERENCES				
SHOOTFLY (YEAR 1)	FOUR-CROP	SORGHUM	MAIZE-SORGHUM					
	21.9	17.6	15.1					
SHOOTFLY (YEAR 2)	FOUR-CROP	SORGHUM		CONTROL	FERTILIZED	[DEFOLIATED]	WATERED	PESTICIDE
	29.6	22.4		33.8	31.2	30.6	27.4	12.9
STALK BORER (YEAR 2)	SORGHUM	FOUR-CROP		FERTILIZED	DEFOLIATED	CONTROL	WATERED	PESTICIDE
	67.3	59.5		85.6	66.4	62.0	61.4	42.2

Figure 93. Sorghum shootfly and stalk borer frequency, Years 1 and 2. Data are percent of plants with symptoms. Year 1 data are from the main control plots. The shootfly census was taken before defoliation and five days after the first pesticide spraying in Year 2. Systems or treatments not sharing a common line are significantly different by Duncan's tests, performed on samples of all systems or treatments combined.

Stalk borer holes were present in 59.5 and 67.3 percent of harvested sorghum stems in the four-crop and sorghum monoculture systems, respectively (Figure 93). Fertilization significantly increased stalk borer damage (23.6 percent greater than controls), pesticide spraying significantly decreased borer damage (19.6 percent less than controls), and the defoliation and watering treatments had no significant effect.

Cowpea Pests and Diseases

Cowpea herbivory by the beetle Ootheca bennigseni (Figure 94) was slightly higher in the four-crop intercrop than in cowpea monoculture in both years, but not significantly so. Herbivory was higher in Year 1 than Year 2. The pesticide treatment significantly reduced Ootheca herbivory compared to controls.

Top necrosis, a leaf disease, was significantly less widespread in cowpea monoculture than in either the maize-cowpea or four-crop system in Year 1; in Year 2 this was reversed, with slightly higher levels in cowpea monoculture than in the four-crop system (Figures 93 and 96). Top necrosis was much more widespread in Year 1 (73-91 percent of plants affected) than in Year 2 (15-22 percent). The stress treatments had no significant effect on top necrosis in Year 2.

Powdery mildew in cowpeas was significantly more prevalent in the maize-cowpea system than in the four-crop system in small plots in Year 1; the trend was the opposite, but not significant, in main plots in the same year. Defoliation had no significant effect on levels of powdery mildew.

The pseudorust Synchitrium was consistently more abundant in cowpea monoculture than in the maize-cowpea and four-crop intercrop systems; the

EXPERIMENT	SYSTEM DIFFERENCES			TREATMENT DIFFERENCES				
YEAR 1 MAIN PLOTS	FOUR-CROP	COWPEA	MAIZE-COWPEA					
	19.5	17.9	16.5					
YEAR 2	FOUR-CROP	COWPEA		FERTILIZED	CONTROL	WATERED	[DEFOLIATED]	PESTICIDE
	8.1	4.6		10.2	9.6	5.6	5.2	.2

Figure 94. Cowpea Ootheca herbivory, Years 1 and 2. Data are percent leaf area missing from the third leaf. Year 1 data are from the main control plots. The census was taken before defoliation and after two pesticide sprayings in Year 2. Systems or treatments not sharing a common line are significantly different by Duncan's tests, performed on samples of all treatments or systems combined.

EXPERIMENT	TOP NECROSIS	POWDERY MILDEW	SYNCHITRIUM
YEAR 1 MAIN PLOTS	FOUR-CROP 90.9; MAIZE-COWPEA 86.3; COWPEA 73.4	FOUR-CROP 28.6; COWPEA 28.5; MAIZE-COWPEA 12.2	COWPEA 13.3; MAIZE-COWPEA 5.9; FOUR-CROP 5.1
YEAR 1 SMALL PLOTS		MAIZE-COWPEA 23.1; COWPEA 12.8; FOUR-CROP 2.8	COWPEA 28.2; FOUR-CROP 3.3; MAIZE-COWPEA 1.9
YEAR 2	COWPEA 21.6; FOUR-CROP 15.2		COWPEA 24.6; FOUR-CROP 15.2

Figure 95. Cowpea top necrosis, powdery mildew, and *Synchitrium* differences among systems, Years 1 and 2. Data are percent of plants with symptoms. Systems not sharing a common line are significantly different by Duncan's tests, performed on samples of all treatments combined in Year 1 small plots and Year 2 (despite slight system-by-treatment interaction in Year 2 for *Synchitrium*, p=.036).

EXPERIMENT	TOP NECROSIS	POWDERY MILDEW	*SYNCHITRIUM*
YEAR 1 SMALL PLOTS		D 13.1, C 12.6	C 13.5, D 8.8
YEAR 2	W 21.0, F 20.3, P 19.1, C 17.0, D 15.5		P 33.1, W 19.2, C 15.4, F 12.3, D 7.8

Figure 96. Cowpea top necrosis, powdery mildew, and *Synchitrium*, differences among treatments, Years 1 and 2. Data are percent of plants with symptoms. Treatments not sharing a common line are significantly different by Duncan's tests, performed on samples of all systems combined despite slight system-by-treatment interaction in *Synchitrium* (p=.036). C=control treatment, F=fertilized; P=pesticide; D=defoliated; W=watered.

difference was significant in Year 1 small plots and in Year 2. Pesticide spraying, which included a fungicide, significantly increased Synchitrium levels in Year 2 compared to controls (33.1 and 15.4 percent of plants affected, respectively). Defoliation consistently reduced Synchitrium levels in both years (nonsignificantly), and watering and fertilization had little effect.

Percent of cowpea seeds having any kind of pest or disease damage was high in both study years, ranging from 85-94 percent (Figure 97). No significant differences among systems were found for three kinds of seed damage (seed shrivelling, seed discoloration, and bruchid holes, Figure 98); seed discoloration was, however, consistently greater in the four-crop intercrop than in cowpea monoculture. Defoliation had no significant effect on any of these three types of damage in either year (Figure 99). The only significant treatment effects were an increase in seed discoloration in the watered plots (compared with pesticide and control plots) and a decrease in bruchid holes in fertilized plots (compared with controls).

Discoloration of cowpea pods was greater in cowpea monoculture than in the maize-cowpea and four-crop systems in Year 1 (by more than 10 percent, not a significant difference, Figures 100 and 101). Pod discoloration was lower in defoliated than control plots (52.0 and 62.5 percent, respectively), but not significantly so. In Year 2, all pods were discolored in all systems and treatments.

Symptoms of scab disease on cowpea pods were significantly more frequent in the cowpea monoculture than in the four-crop intercrop (Year 2). Treatment effects were not significant, but pesticide-sprayed plots had 11.6 percent greater scab occurrence than controls.

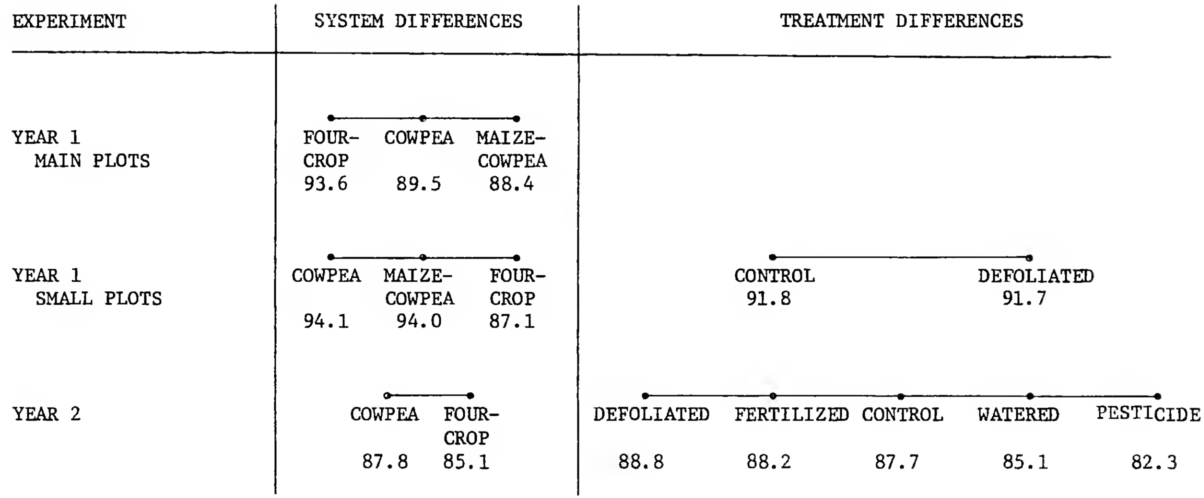

Figure 97. Cowpea seed damage of any kind, Years 1 and 2. Data are percent of seeds damaged. Systems or treatments connected by a common line are not significantly different by Duncan's tests, performed on samples of all systems or treatments combined.

EXPERIMENT	SEED SHRIVELLING			SEED DISCOLORATION			BRUCHID HOLES		
YEAR 1 MAIN PLOTS	FOUR-CROP 48.2	COWPEA 44.6	MAIZE-COWPEA 28.6	FOUR-CROP 47.0	COWPEA 42.9	MAIZE-COWPEA 33.1	COWPEA 15.2	FOUR-CROP 8.5	MAIZE-COWPEA 5.0
YEAR 1 SMALL PLOTS	FOUR-CROP 41.9	MAIZE-COWPEA 35.5	COWPEA 31.7	FOUR-CROP 40.1	MAIZE-COWPEA 39.9	COWPEA 30.6	MAIZE-COWPEA 8.3	FOUR-CROP 6.5	COWPEA 5.9
YEAR 2	COWPEA 72.6	FOUR-CROP 66.2		FOUR-CROP 79.4	COWPEA 74.0		FOUR-CROP 4.7	COWPEA 3.0	

Figure 98. Cowpea seed shrivelling, seed discoloration, and bruchid holes, differences among systems, Years 1 and 2. Data are percent of seeds with symptoms. Systems connected by a common line are not significantly different by Duncan's tests, performed on samples of all treatments combined despite slight system-by-treatment interaction in seed discoloration (p=.04).

EXPERIMENT	SEED SHRIVELLING	SEED DISCOLORATION	BRUCHID HOLES
YEAR 1 SMALL PLOTS	D 36.6, C 36.1	C 38.8, D 35.0	C 7.2, D 6.6
YEAR 2	F 77.5, D 75.0, W 67.4, P 66.9, C 62.3	W 92.4, F 83.7, D 79.2, P 66.8, C 66.6	C 5.6, W 4.3, P 4.0, D 3.4, F 1.6

Figure 99. Cowpea seed shrivelling, seed discoloration, and bruchid holes, differences among treatments, Years 1 and 2. Data are percent of seeds with symptoms. C=control treatment; F=fertilized, P=pesticide; D=defoliated; W=watered. Treatments not sharing a common line are significantly different by Duncan's tests, performed on samples of all systems combined despite slight system-by-treatment interaction in seed discoloration (p=.04).

EXPERIMENT	POD DISCOLORATION (percent pods)			POD SCAB (percent pods)		APHIDS (percent plants)		
YEAR 1 MAIN PLOTS	COWPEA 73.4	FOUR-CROP 63.5	MAIZE-COWPEA 61.7			COWPEA 23.6	MAIZE-COWPEA 13.2	FOUR-CROP 10.9
YEAR 1 SMALL PLOTS	COWPEA 65.5	MAIZE-COWPEA 55.0	FOUR-CROP 51.2			MAIZE-COWPEA 31.1	COWPEA 21.4	FOUR-CROP 18.4
YEAR 2	COWPEA 100.0	FOUR-CROP 100.0		COWPEA 51.1	FOUR-CROP 36.3	COWPEA 2.6	FOUR-CROP 2.2	

Figure 100. Cowpea pod discoloration, pod scab, and aphids, differences among systems, Years 1 and 2. Systems not sharing a common line are significantly different by Duncan's tests, performed on samples of all treatments combined.

EXPERIMENT	POD DISCOLORATION (percent pods)	POD SCAB (percent pods)	APHIDS (percent plants)
YEAR 1 SMALL PLOTS	C 62.5, D 52.0		C 34.1, D 13.1
YEAR 2	C F P D W 100.0	P 54.4, W 46.5, C 42.8, D 39.9, F 35.9	C 3.3, F 2.5, W 2.3, P .6

Figure 101. Cowpea pod discoloration, pod scab, and aphids, differences among treatments, Years 1 and 2. C=control treatment; F=fertilized; D=defoliated; P=pesticide; W=watered. Treatments not sharing a common line are significantly different by Duncan's tests, performed on samples of all systems combined.

Aphid populations were consistently, but nonsignificantly, lower in the four-crop system than in either the cowpea monoculture or maize-cowpea intercrop. Aphids were more abundant in Year 1 than Year 2. Defoliated plots had significantly fewer aphids than controls in Year 1; no significant differences were found in Year 2.

The flower- and seed-feeding Lepidopteran *Maruca testiculatis* was inventoried by counts of larvae in flowers, holes in pods, and holes in seeds (Figures 102 and 103). *Maruca* was consistently more abundant in the four-crop system than in cowpea monoculture for all three measures in both years; in no case, however, was the difference statistically significant. Fertilization significantly increased percent seeds with *Maruca* holes (compared with the control, defoliated, and pesticide plots). Watering increased levels of all three variables but not significantly. Pesticide spraying had no significant effect on *Maruca* levels; percent flowers with larvae was unchanged, percent damaged pods increased slightly, and percent damaged seeds decreased slightly in sprayed plots compared with controls.

Pumpkin Pests and Diseases

Pumpkin melonfly damage to fruits (Figure 104) was lower by approximately 30 percent in the maize-pumpkin system than in either the four-crop or pumpkin monoculture systems in Year 1; the difference was not significant due to high variability among plots. Melonfly damage was greater in Year 1 than Year 2 in pumpkin monoculture systems. (Fruit yield was zero in the four-crop system in Year 2.) The pesticide treatment significantly reduced melonfly levels compared with controls in Year 2.

EXPERIMENT	*MARUCA* LARVAE IN FLOWERS (percent flowers)	POD *MARUCA* HOLES (percent pods)	SEED *MARUCA* DAMAGE (percent seeds)
YEAR 1 MAIN PLOTS		FOUR-CROP 34.3 COWPEA 31.8 MAIZE-COWPEA 29.1	FOUR-CROP 7.3 COWPEA 7.3 MAIZE-COWPEA 5.5
YEAR 1 SMALL PLOTS		FOUR-CROP 36.7 COWPEA 34.2 MAIZE-COWPEA 25.8	MAIZE-COWPEA 4.9 FOUR-CROP 4.5 COWPEA 3.9
YEAR 2	FOUR-CROP 37.2 COWPEA 30.4	FOUR-CROP 18.2 COWPEA 16.3	FOUR-CROP 18.2 COWPEA 16.3

Figure 102. Cowpea *Maruca* larvae, pod exit holes, and seed damage, differences among systems, Years 1 and 2. Systems sharing a common line are significantly different by Duncan's tests, performed on samples of all treatments combined.

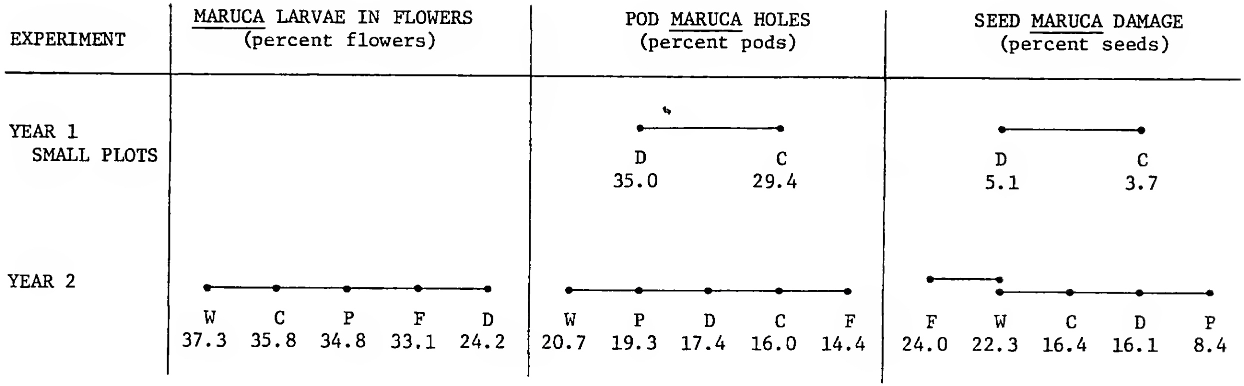

Figure 103. Cowpea _Maruca_ larvae, pod exit holes, and seed damage, differences among treatments, Years 1 and 2. C=control treatment; F=fertilized; D=defoliated; W=watered. Treatments not sharing a common line are significantly different by Duncan's tests, performed on samples of all systems combined.

PEST OR DISEASE	SYSTEM DIFFERENCES			TREATMENT DIFFERENCES				
MELONFLY (YEAR 1)	FOUR-CROP 60.7	PUMPKIN 59.4	MAIZE-PUMPKIN 27.7					
MELONFLY (YEAR 2)		PUMPKIN 38.4		CONTROL 57.0	DEFOLIATED 41.2	WATERED 37.8	FERTILIZED 33.3	PESTICIDE 19.7
LEAF DISCOLORATION (YEAR 1)	MAIZE-PUMPKIN 89.7	PUMPKIN 87.6	FOUR-CROP 72.6					

Figure 104. Pumpkin melonfly and leaf discoloration, Years 1 and 2. Data are percent of fruits with melonfly symptoms and percent of plants with > 5 discolored leaves. Systems or treatments not sharing a common line are significantly different by Duncan's tests. The Duncan's test for treatment differences were based on the pumpkin monoculture only, since the four-crop system yielded no pumpkin fruits.

Pumpkin leaf discoloration (Figure 104) was lower in the four-crop system than in the maize-pumpkin and pumpkin monoculture systems in Year 2, but not significantly so.

Summary of Pests and Diseases in Intercrops and Monocultures

Levels of most pests of the four agronomic species were unaffected by system diversity (Tables 60-63). None of the maize or pumpkin pests inventoried were significantly more or less abundant in intercropping systems, and no clear trends were seen for those pest communities as a whole, although pest levels tended to be high in the maize-pumpkin system in Year 1. Shootfly was the only sorghum pest to vary significantly among systems; its frequency was greater in the four-crop system in both years, significantly so in Year 2. No clear trends were apparent for sorghum pests as a whole. The sum of ranks of cowpea pest levels was higher in the maize-cowpea system than in the four-crop or cowpea monoculture systems. Otherwise, there were no clear trends for cowpea pests as a community. Cowpea *Synchitrium* and pod scab, however, tended to be more abundant in the simple cowpea monoculture. Top necrosis was significantly more abundant in intercrop systems than in monoculture in Year 1, but was more abundant in monoculture in Year 2.

Effects of Pests on Productivity

Strong correlations of pests and diseases with productivity would suggest either that pests were responsible for changes in productivity or that differences in productivity influenced pest levels. Lack of correlation implies that either pest and productivity levels do not

Table 60. Summary of system differences in maize lodging, pests and diseases, Years 1 and 2. Values are rankings of systems by pest level in control plots: 1 = highest value. No significant differences among systems were found for any variable in either year by Duncan's tests.

SYSTEM	LODGING	STRIGA	STREAK VIRUS	STALK BORER
YEAR 1				
MAIZE	3	6	3	
SPARSE MAIZE	4	5	6	
MAIZE-SORGHUM	5	2	4	
MAIZE-COWPEA	1	4	5	
MAIZE-PUMPKIN	2	1	1	
FOUR-CROP	6	3	2	
YEAR 2				
MAIZE	1		1	2
FOUR-CROP	2		2	1

Table 61. Summary of system differences in sorghum lodging, pests and diseases, Years 1 and 2. Values are rankings of systems by pest level in control plots; 1 = highest value. The only significant difference among systems by Duncan's tests was in Year 2 shootfly levels (see Results).

SYSTEM	LODGING	STRIGA	SHOOTFLY	STALK BORER
YEAR 1				
SORGHUM	2	3	2	
MAIZE-SORGHUM	3	1	3	
FOUR-CROP	1	2	1	
YEAR 2				
SORGHUM	2		2	1
FOUR-CROP	1		1	2

Table 62. Summary of system differences in cowpea pests and diseases, Years 1 and 2. Values are rankings of systems by pest level in control plots; 1 = highest value. Significant differences were found among systems by Duncan's tests in Year 1 and Year 2 top necrosis, Year 1 pod scab, and Year 2 *Synchitrium* levels (see Results).

	OOTHECA	TOP NECROSIS	POWDERY MILDEW	*SYNCHITRIUM*	SHRIVELLING (seeds)	DISCOLORATION (seeds)	BRUCHIDS (seeds)	ANY DAMAGE (seeds)	DISCOLORATION (pods)	SCAB (pods)	APHIDS	*MARUCA* (flowers)	*MARUCA* (pods)	*MARUCA* (seeds)	SUMMED RANKS
YEAR 1															
COWPEA	2	3	2	1	2	2	1	2	1		1		2	2	19
MAIZE-COWPEA	3	2	3	2	3	3	3	3	3		2		3	3	30
FOUR-CROP	1	1	1	3	1	1	2	1	2		3		1	1	17
YEAR 2															
COWPEA	2	1	1	1	2	2	1	1	1	1	1	2	2	2	15
FOUR-CROP	1	2	2	2	1	1	2	2	2	2	2	1	1	1	18

Table 63. Summary of system differences in pumpkin pests and diseases, Year 1. Values are rankings of systems by pest level in control plots; 1 = highest value. No significant differences were found among systems for either variable by Duncan's tests.

SYSTEM	MELONFLY	LEAF DISCOLORATION
PUMPKIN	2	2
MAIZE-PUMPKIN	3	1
FOUR-CROP	1	3

interact or that the range of variation of one or both variables was too small, or uncontrolled factors too influential, to detect the relationship. In this study the relationship between pest levels and yield was examined by three methods. First, year-to-year differences in pest levels and their relationships with year-to-year yield differences were assessed. Second, the degree of correlation of pest levels with productivity (by plot) in the separate Year 1 and Year 2 experiments was determined. Finally, response of both pest and productivity levels to the stress treatments was used to evaluate the degree to which pests and productivity covary.

Weeds

Weeds were more abundant in Year 2 than Year 1 (Table 64) but biomass at harvest of most systems was approximately the same in both years. Weed biomass in the first and second weeding samples was not consistently correlated with any productivity variable except full-standedness in the first Year 1 weeding sample (Table 65). In the third weeding, however, weed growth was highly negatively correlated with all productivity measures except Year 1 LAI and canopy cover. The low correlation of weed growth with those measures was probably due to abundant weed growth in the high-canopy-cover cowpea monoculture. Weed growth was uncorrelated with root/shoot and allocation ratios, and was not significantly different from controls in the fertilization and watered treatments (Table 66).

Table 64. Summary of levels of natural stressors in Years 1 and 2. Mean and standard deviation (s) are given; units are as described in the Results section. Only variables measured in both years are included, and the data are from control plots only.

		YEAR 1		YEAR 2	
SPECIES	PEST	MEAN	s	MEAN	s
MAIZE	LODGING	3.2	2.5	12.5	10.8
	STREAK	14.0	5.2	16.8	4.9
SORGHUM	LODGING	.4	.4	1.0	.9
	SHOOTFLY	18.2	4.2	33.8	10.5
PUMPKIN	MELONFLY	47.9	23.6	22.8	34.5
COWPEA	OOTHECA	17.9	4.2	9.6	9.7
	TOP NECROSIS	83.5	8.5	17.0	9.1
	SYNCHITRIUM	8.1	7.9	15.4	8.1
	APHIDS	15.9	10.7	3.3	6.2
	SEED BRUCHIDS	9.6	6.9	5.6	4.1
	SEED SHRIVELLING	40.5	11.1	62.3	18.2
	SEED DISCOLORATION	41.0	19.1	66.6	13.0
	UNDAMAGED SEEDS	9.5	3.8	12.3	3.9
	MARUCA (pods)	31.7	6.1	14.2	11.0
	MARUCA (seeds)	6.7	1.8	16.5	5.4
ALL SYSTEMS	WEEDS[a]	.3	.1	8.8	3.5
COMBINED	WEEDS[b]	40.2	79.8	118.5	73.4

[a] second weeding

[b] third weeding

Table 65. Correlations of weed growth with other productivity measures, Years 1 and 2. Experiment 1 = Year 1 main plots; 2 = Year 1 small plots; 3 = all Year 2 plots. Weeding 1, 2 and 3 = first, second, and third weed samples. Values are Pearson product-moment correlation coefficients, based on all plots (of all systems and treatments) in which the measures were taken.

	EXPERIMENT	BIOMASS[a]	BIOMASS[b]	EDIBLE BIOMASS[a]	LAI[c]	LAI[b]	CANOPY COVER[c]	FULLSTANDEDNESS[d]	PERCENT MONOCOT LAI[c]	ROOT BIOMASS[b]	ROOT/SHOOT[b]	ALLOCATION RATIO[a]
WEEDS 1	1	.12		-.03	-.18		-.14	-.54†	-.11			
WEEDS 2	1	.06		.13	-.13		-.09	-.21	-.01			
	3	.08	.24	.25	.15	.32	.18	-.27	-.14	.16	-.04	.33
WEEDS 3	1	-.66†		-.52†	-.07		.10	-.56†	-.59†			
	3	-.53†	-.46†	-.48†	-.45†	-.43†	-.56†	-.55†	-.59†	-.35†	.26	-.10

[a]at final harvest

[b]at flowering

[c]second LAI/canopy cover sample

[d]third stand count

†significant at $p < .05$

Table 66. Summary of effects of stress treatments on lodging, pests and diseases, Years 1 and 2. x = nonsignificant increase (+) or decrease (-) in pests compared with the control treatment; s = significant increase or decrease compared with controls.

SPECIES PEST	FERTILIZED		PESTICIDE		WATERED		DEFOLIATED		(YEAR 1) DEFOLIATED	
	+	-	+	-	+	-	+	-	+	-
MAIZE										
LODGING										X
STALK BORER	X					X				
STREAT		X		X	X		X			
SORGHUM										
LODGING									X	
SHOOTFLY		X		S		X				
STALK BORER	S			S		X		X		
COWPEA										
OOTHECA	X			S		X				
TOP NECROSIS	X		X		X			X		
POWDERY MILDEW									X	
SYNCHITRIUM		X	S		X			X		X
APHIDS		X		X		X				S
SEED SHIVELLING	X		X		X		X		X	
SEED DISCOLORATION	X		X		X		X			X
SEED BRUCHIDS		S		X		X		X		X
ANY SEED DAMAGE	X			X		X	X			X
POD DISCOLORATION										X
POD SCAB		X	X		X			X		
MARUCA (flowers)		X		X	X			X		
MARUCA (pods)		X	X		X		X		X	
MARUCA (seeds)	X			X	X			X	X	
PUMPKIN										
MELONFLY		X		S		X		X		
ALL SYSTEMS COMBINED										
WEEDS[a]	X				X					
TOTAL	9	9	6	10	10	8	5	8	5	7

[a]third weeding

Maize and sorghum pests

Maize lodging, sorghum lodging, and maize streak infestation were slightly higher in Year 2 than Year 1, but this did not correspond with any marked difference in productivity in the two years. Lodging of both maize and sorghum tended to be positively correlated with edible and total biomass and negatively correlated with mortality, probably due to the tendency of taller, heavier plants with high leaf area to lodge. Mortality was negatively correlated with other productivity variables, and probably did not directly influence lodging rate or vice-versa.

The stress treatments had no significant effect on any maize pests sampled (Table 66). Fertilization and pesticide spraying nonsignificantly reduced levels of streak virus. Maize stalk borers were more abundant in fertilized plots than in controls, as were sorghum stalk borers (significantly). Despite the high levels of borers in maize and sorghum (8-9 percent of young maize plants windowed and 42-86 percent of harvested sorghum stems infested), it was not clear that these pests reduced yields of the two crops significantly. Maize and sorghum stalk borer levels were slightly positively correlated with edible and total biomass (Tables 67 and 68); this may have been an indirect relationship caused by the higher borer levels in fertilized plots. Alternatively, the borers may have stimulated maize and sorghum productivity. Sorghum LAI and biomass were neutrally or slightly negatively affected by pesticide spraying, as would be expected if this were true. (Borer levels were significantly lower in sprayed than control plots.) Fertilized plots had higher stalk borer levels than controls, and were

Table 67. Correlations of maize natural stressors with edible and total biomass and mortality, Years 1 and 2. Experiment 1 = Year 1 main plots; 2 = Year 1 control and defoliated plots; 3 = all Year 2 plots. Values are Pearson product-moment correlation coefficients. No correlations were statistically significant.

STRESSOR	EXPERIMENT	BIOMASS[a]	EDIBLE BIOMASS[a]	MORTALITY[b]
STALK BORER	3	.23	.15	.27
LODGING	1	.38	.40	-.26
STREAK VIRUS	1	.27	.18	-.07
	3	-.20	-.07	-.09
STRIGA	1	-.19	-.21	.19
	2	-.28	-.33	

[a]at final harvest

[b]days 24-74, Year 1; days 28-96, Year 2

Table 68. Correlation of sorghum natural stressors with edible and total biomass and mortality, Years 1 and 2. Experiment 1 = Year 1 main plots; 2 = Year 1 control and defoliated plots; 3 = all Year 2 plots. Values are Pearson product-moment correlation coefficients.

STRESSOR	EXPERIMENT	BIOMASS[a]	EDIBLE BIOMASS[a]	MORTALITY[b]
STALK BORER	3	.30†	.11	.15
SHOOTFLY	1	.05	.08	-.57
	3	.28†	.09	.14
LODGING	1	.18	.09	-.17
	3	.03	.05	-.09
STRIGA	1	.00	.06	.03
	2	.17	.22	

[a] at final harvest

[b] days 24-74, Year 1 and days 28-96, Year 2

† significant at $p < .05$

also more productive, but this was almost certainly due to increased nutrient levels. The only indication that stalk borers may have reduced productivity was their slight positive correlation with both maize and sorghum mortality. The effect of borers on maize and sorghum productivity was not, therefore, completely clear, but most evidence indicated increased yields due to high borer levels. Several lines of analysis also indicated that shootfly infestation may have stimulated biomass production in sorghum. Shootfly frequency was higher in Year 2 than Year 1; sorghum productivity was also slightly higher in Year 2. Among plots in Year 2, shootfly levels were significantly positively correlated with biomass production. Shootfly levels were negatively correlated with mortality in Year 1 (as expected if shootflies stimulate productivity); no clear relationahip with mortality was found in Year 2.

Damage by the sorghum shootfly has been associated with increased tillering (de Pury 1974). The high correlation of both sorghum stalk borer and shootfly levels with tillering suggested that both these pests may have caused tillering in sorghum. Tillering was highly correlated with edible and total biomass in control plots in both study years; it was reduced in the pesticide treatment, where stalk borers and shootfly frequencies were also reduced; and it was increased in the fertilization treatment, where stalk borers were more abundant than in controls. Greater tillering in fertilized plots may have also been due to high levels of nitrogen (Blackman and Templeman 1938). Only in the year-to-year comparison was the link between tillering and productivity less clear; tillering frequency was high and approximately equal in both

years (mean 54 and 47 percent in Years 1 and 2), and sorghum productivity was slightly higher in Year 2 than Year 1.

Cowpea pests

Cowpea pests were numerous and abundant in both study years; those sampled represent only a fraction of the pests and diseases present. The large response of cowpea to the pesticide treatment is perhaps the best evidence that pests and diseases are an important factor limiting cowpea productivity. Cowpea biomass increased 466 percent and LAI increased 508 percent in Year 2 sprayed monoculture plots compared with controls. Although the absolute increase was about the same in intercrop and monoculture, yield was higher in the four-crop system, so the percent yield increase by spraying was much lower in intercrop than monoculture.

Cowpea edible and total biomass were higher in Year 2 than in Year 1, but the pests and diseases sampled were not consistently more abundant in Year 1 (Table 64). The high midseason cowpea LAI and canopy cover but low harvest in Year 1 compared with Year 2 were probably due to delayed effects of pest and disease attack, especially top necrosis, that affected over 90 percent of cowpea plants in some Year 1 plots. Reduced levels of top necrosis, *Ootheca* herbivory, and aphids in Year 2 may have been partially responsible for the greater cowpea yield in Year 2.

Levels of several cowpea pests were significantly correlated with biomass, edible biomass, and mortality in Year 2 in a sample of all treatments (Table 69). Aphids, *Ootheca* herbivory, *Maruca* holes in seeds,

Table 69. Correlations of cowpea pests and diseases with edible and total biomass and mortality, Years 1 and 2. Experiment 1 = Year 1 main plots; 2 = Year 1 control and defoliated plots; 3 = all Year 2 plots. Values are Pearson product-moment correlation coefficients.

	EXPERIMENT	BIOMASS[a]	EDIBLE BIOMASS[a]	MORTALITY[b]
APHIDS	1	-.01	-.80	-.20
	2	-.14	.17	
	3	-.33†	-.08	.27
OOTHECA	1	-.09	-.83‡	-.41
	3	-.39‡	-.36	.60‡
POWDERY MILDEW	1	.82‡	.23	.29
	2	-.11	-.01	
SYNCHITRIUM	1	.10	.29	-.13
	2	-.30	-.08	
	3	.25	.24	-.50‡
TOP NECROSIS	1	.15	.17	.29
	3	.02	-.13	-.19
MARUCA (flowers)	3	-.09	-.10	.00
MARUCA (seeds)	1	.43	-.39	.24
	2	-.24	-.05	
	3	-.36†	-.46‡	.23
MARUCA (pods)	1	-.11	-.57	-.40
	2	-.02	-.12	
	3	.39‡	.14	-.01
POD DISCOLORATION	1	.04	-.15	-.49
	2	-.12	.17	
POD SCAB	3	-.31†	-.25	-.37†
SEED BRUCHIDS	1	.47	-.04	.15
	2	-.12	-.12	
	3	-.27	-.03	.03
SEED DISCOLORATION	1	.40	-.27	.36
	2	.36	.08	
	3	-.16	-.27	-.07
SEED SHRIVELLING	1	.52	-.44	.36
	2	.38	.34	
	3	-.09	-.11	.09

[a] at first harvest

[b] days 24–74, Year 1, days 28–96, Year 2

† significant at $p < .05$

‡ significant at $p < .01$

and pod scab were significantly negatively correlated with edible and/or total biomass, but Maruca holes in pods and powdery mildew were significantly correlated with mortality. Levels of top necrosis, Synchitrium, and pod scab were significantly higher in the low-productivity cowpea monoculture than in the four-crop intercrop. These results indicate that the above pests (excluding Maruca, for which the data are inconclusive) either reduce cowpea productivity or preferentially attack low productivity stands.

Most of the cowpea pests and diseases sampled did not respond significantly to the stress treatments (Table 66), but the large response of cowpea productivity to spraying indicates that pests and/or diseases do strongly limit cowpea productivity. Some important cowpea pests that might have been responsible for yield depression, such as nematodes and thrips, were not measured. Ootheca herbivory was significantly reduced in pesticide-sprayed plots, but Synchitrium levels increased, for unknown reasons. Bruchid damage to seeds decreased with fertilization, again, for unknown reasons. Aphids were significantly reduced by defoliation in Year 1.

Of the cowpea pests and diseases sampled, then, there was evidence for pest-productivity interaction for aphids, Ootheca beetles, pod scab, top necrosis, and Synchitrium. These and other, unmeasured, pests were likely to be responsible for differences in cowpea productivity among systems.

Pumpkin pests

The high pumpkin edible yield in Year 2 (despite lower stand counts, LAI, canopy cover, and total biomass) was almost certainly due

to reduced melonfly populations. Fruits were set in the Year 1 crop but did not reach maturity due to melonfly attack and entry of rot through oviposition holes. (Only edible pumpkin yield of monocultures could be compared, since it was zero in the four-crop system in both years.) Among Year 2 monoculture plots melonfly levels were not significantly correlated with edible biomass, total biomass, or mortality (Table 70). Melonfly levels were significantly reduced by pesticide spraying, but edible and total biomass and LAI declined to nearly zero regardless; the combination of diazinon and dimecron sprayed on day 28 appears to have been phytotoxic. Leaf discoloration in pumpkin was not significantly related to total biomass, edible biomass, or mortality in Year 2 plots.

Summary of Diversity-Pest Level-Productivity Relationships

The effects of intercropping on pest levels, and the several types of data relating pest levels to productivity, are summarized in Table 71. Maize productivity was apparently not influenced by pest levels. Sorghum productivity was slightly stimulated by shootfly and stalk borers. Cowpea productivity was limited by pest levels but the specific pests responsible could not be conclusively identified. *Ootheca*, aphids, and pod scab appeared to be partially responsible for low cowpea productivity. Leaf diseases (top necrosis, powdery mildew, and *Synchitrium*) were positively correlated with productivity, possibly due to resource concentration and microclimate effects. Other measures of cowpea pest damage were not conclusive; *Maruca* effects on productivity by several measures were inconsistent. Pumpkin edible yield was strongly related to melonfly frequency. Melonfly infestation

Table 70. Correlations of pumpkin pests and diseases with edible and total biomass and mortality, Years 1 and 2. Experiment 1 = Year 1 main plots; 2 = Year 1 control and defoliated plots; 3 = all Year 2 plots. Values are Pearson product-moment correlation coefficients. No correlations were statistically significant.

STRESSOR	EXPERIMENT	BIOMASS[a]	EDIBLE BIOMASS[a]	MORTALITY[b]
MELONFLY[c]	1	.31		-.13
	2	-.21		
	3	.03	.04	.37
LEAF DISCOLORATION	1	.15		-.31

[a]at final harvest

[b]days 24-74, Year 1; days 28-96, Year 2

[c]pumpkin monoculture only (edible yield = 0 in all four-crop plots)

Table 71. Summary of pest-productivity relationships. 0 = nonsignificant correlation or treatment effect: + or - = significant positive or negative effect, except for year-to-year differences, which were not subjected to statistical tests.

CROP / PEST	YEAR 2 - YEAR 1: PESTS	YEAR 2 - YEAR 1: BIOMASS	PEST/BIOMASS CORRELATIONS: YEAR 1	PEST/BIOMASS CORRELATIONS: YEAR 2	PESTICIDE EFFECTS ON: PEST	PESTICIDE EFFECTS ON: BIOMASS	INTERCROPPING EFFECTS
MAIZE							
LODGING	+	=	0			0	0
STRIGA			0	0			0
STREAK	+		0		0		0
BORER			0				0
SORGHUM							
LODGING	+	+	0	0		0	0
STRIGA			0				0
SHOOTFLY	+		0	+	-		+
BORER				+	-		0
COWPEA							
OOTHECA	-	+	0	-	-	+	0
TOP NECROSIS	-		0	+	0		+(Yr1)/-(Yr2)
POWDERY MILDEW			+				0
SYNCHITRIUM	+		0	0	+		-
APHIDS	-		0	-	0		0
SEED SHRIVELLING	+		0	0	0		0
SEED DISCOLORATION	+		0	0	0		0
SEED BRUCHIDS			0	0	0		0
ANY SEED DAMAGE	-				0		0
POD DISCOLORATION			0				0
POD SCAB			-		0		-
MARUCA (flowers)				0	0		0
MARUCA (pods)	-		0	+	0		0
MARUCA (seeds)	+		0	-	0		0
PUMPKIN							
MELONFLY	-	-(total)	0	0	-	0	0
LEAF DISCOLORATION		+(edible)	0				0
ALL SYSTEMS COMBINED							
WEEDS	+	=	-	-			-(some systems)

[a]third weeding

was reduced in pesticide-sprayed plots, but the effect of that reduction on productivity was complicated by pesticide phytotoxicity. Weed levels were highly negatively correlated with productivity within years, but not between years.

Significant intercropping effects were few: sorghum shootfly and Year 1 cowpea top necrosis were more abundant in intercrop than monoculture (both being positively related to productivity, also), but Year 2 top necrosis, Synchitrium, and pod scab were more abundant in monocultures. Of the latter three pests only pod scab was negatively related to productivity by other measures.

The maize productivity increases in intercrop, which were largely responsible for the intercrop/monoculture differences, were probably not caused by pests and diseases. Sorghum productivity in intercrop was apparently slightly stimulated by higher shootfly frequency than in monoculture. There was no evidence that the cowpea productivity increase in intercrop compared with monoculture was due to differing levels of any of the pests monitored, but it is likely, judging from the pesticide response, that it was due at least partly to levels of other pests or diseases that were not measured. Pumpkin total biomass was not related to either of the two types of damage measured, but edible yield was strongly influenced by melonfly attack, which could partly explain differences in edible (but not total) yield differences in intercrop and monoculture.

Pest Stability

No evidence was found in this study for increased stability of pest populations in the diverse four-crop system compared with monocultures.

Coefficient of variation of pest levels was calculated for year-to-year fluctuations and fluctuations among control plots in Years 1 and 2, and percent change from controls in the fertilized and pesticide-sprayed plots was evaluated. The four-crop and monoculture systems were ranked for each pest by each type of stability index (Table 72). No clear trends were evident; of 83 comparisons, stability of pest levels in intercrop was the same or greater than that of monoculture in almost exactly half (39), and results for each pest were also inconsistent. One exception was maize streak, which was consistently more stable in monoculture than intercrop. Although the year-to-year and Year 1 among-plot coefficients of variation are based on small samples (n = 2 and 3, respectively), each sample is based on a census of a large number of plants. The other three indices are based on larger numbers of samples (4-6 plot means), each of which is a good estimator of pest activity on a given plot. The coefficients of variation obtained should therefore be reasonably good estimators of pest (in)stability.

Discussion

Previous Studies

Effects of intercropping on several of the pests censused in this study have been studied previously. The green color of peanuts was thought to reduce attraction of stalk borers for oviposition in a maize-peanut intercrop (IRRI 1974). In this study maize stalk borers were (nonsignificantly) more abundant in monocultures, but sorghum borers were more abundant in intercrop. Consistently higher levels of borers

Table 72. Summary of comparisons of pest stability in intercrops and monocultures. I = lower coefficient of variation or lower response to fertilizer or pesticide (greater stability) in the four-crop intercrop than in monoculture. M = greater stability in monoculture than in the four-crop system. Weed stability in the intercrop is compared with that of corresponding monocultures. Eq = equal coefficients of variation.

SPECIES PEST	YEAR-TO-YEAR FLUCTUATIONS	FLUCTUATIONS AMONG PLOTS, YEAR 1	FLUCTUATIONS AMONG PLOTS, YEAR 2	RESPONSE TO FERTILIZATION (% control)	RESPONSE TO PESTICIDE (% control)
MAIZE					
LODGING	M	--	I	--	--
BORER	--	--	M	I	I
STREAK	Eq.	M	M	M	M
SORGHUM					
LODGING	I	M	M	--	--
SHOOTFLY	M	I	I	M	I
STALK BORER	--	--	I	M	I
COWPEA					
<u>OOTHECA</u>	I	I	M	I	M
TOP NECROSIS	M	I	I	I	I
POWDERY MILDEW	--	I	--	--	--
<u>SYNCHITRIUM</u>	M	M	I	M	I
APHIDS	I	M	M	M	I
SEED SHRIVELLING	I	M	I	I	I
SEED BRUCHIDS	I	I	I	M	I
SEED DISCOLORATION	I	M	M	M	Eq.
UNDAMAGED SEEDS	M	I	M	M	M
POD DISCOLORATION	--	M	--	--	--
POD SCAB	--	--	M	I	I
<u>MARUCA</u> (flower)	--	--	M	M	I
<u>MARUCA</u> (pods)	M	M	M	M	M
<u>MARUCA</u> (seeds)	I	M	I	M	I
PUMPKIN					
MELONFLY	--	M	--	--	--
LEAF DISCOLORATION	--	M	--	--	--
ALL SYSTEMS COMBINED					
WEEDS[a]	M	--	--	M	--

[a]third weeding

in fertilized plots may be a response to increased greenery, however. The Cicadulina leafhopper that carries maize streak virus is thought to be more mobile across nonhost plants than across bare ground (Rose 1978), suggesting a density, but not necessarily a diversity, effect. Leafhoppers also prefer diseased plants, presumably due to high levels of tissue nitrogen. Streak did not vary significantly among systems or stress treatments in this study.

Germination of the plant parasite Striga is thought to be stimulated by root exudates (Ivens 1975); nonhosts such as peanut are sometimes used as trap crops. Soil storage of Striga seeds is large, however, so triggering of germination by nonhosts in an intercrop would not be expected to reduce parasitism on host plants. In this study no significant differences in Striga abundance were found between intercrops and monocultures.

Bean aphid infestations tend to be worse in dry weather (de Pury 1974); the consistently greater levels of aphids in monocultures (and Synchitrium, which appeared to grow on aphid honeydew) may have been related to differences in microclimate.

Pumpkin melonfly is attracted to maize tassels, and maize is sometimes used as a trap crop for the pest (de Pury 1974). Melonfly levels in this study were lowest in the maize-pumpkin intercrop, where potential for melonfly trapping within the system was greatest; the difference was not significant, however.

Pest Levels

The theoretical effects of habitat diversity on pest and disease levels have not been resolved, and the results of this study support

the conclusion that the effects of increasing diversity are highly pest- and ecosystem-specific. Neither intercropping nor monoculture systems were clearly better from a standpoint of pest and disease levels, and examples of both significantly higher and lower pests in the diverse system were found.

One natural stressor that was clearly lower in intercrops than in corresponding monocultures was weed competition. Reduced weed groth in the intercrops (compared with a mean of corresponding monocultures) probably reflects higher levels of competition from crops, as indicated by the negative correlation of weed growth with crop LAI and total biomass. Presence of a nitrogen fixing species (cowpea) also seemed to be associated with intercrop advantage in terms of weed growth. The cowpea monoculture had high levels of weed growth in both years; mixing it with other species in the intercrop systems was advantageous.

Low crop productivity probably permitted weed growth to a greater extent than the low weed growth permitted greater crop productivity. Over a period of years, however, or in poorly weeded crop systems, weed growth could inhibit crop productivity. Increased weed growth in Year 2 supports the conventional wisdom that weeds build up over time in tropical agroecosystems.

Interpretation of pest and disease data is complicated by the so-called dilution effect (Pimentel 1961a). In monoculture a given number of pests per unit area (insects, spores, etc.) may inflict less damage to individual plants than would the same population in an intercrop system. Equal populations on a per-ground-area basis would be lower on a per-plant or per-leaf-area basis in monocultures than in

intercrops. Productivity responses should be related to per-plant, rather than per-area measures. The finding that pest levels measured on a per-plant basis (all but Striga and weeds) did not usually vary significantly with diversity means that pest populations on a per-ground-area basis were probably higher in monocultures than in the intercrops in some cases.

Pest Stability

Habitat diversity has been said to stabilize predator-prey interactions by several mechanisms, but this generalization is far from having been proven (de Loach 1970, Murdoch 1975, Murdoch and Oaten 1975). Stabilization of pest populations through diversity effects could account for reduced fluctuations in plant productivity, when pests constitute a significant drain or stimulus to productivity. Alternatively, pests may act as regulators of plant productivity, so that decreased pest stability could be associated with increased plant yield stability.

The lack of clear trends in this study regarding pest levels and pest stabilities in simple and diverse systems should not be taken as a refutation of theories regarding pest regulation by mechanisms related to diversity, or plant productivity regulation by consumers. Agricultural systems may lack stabilizing mechanisms present in naturally coevolved systems (Huffaker 1974, Goodman 1975, Murdoch 1975, Strong 1979). If resource limitations determine pest levels and density-dependent natural enemy effects are responsible for stability differences (Root 1973, van Emden and Williams 1974), then the generally high productivity and palatability of crop systems, and the possible weakness of coevolved

natural enemy relationships, could account for the uniformly high and unstable levels of pests found in this study.

Plot Size, and the Range of Diversity Tested

Effects of plot size in relation to pest movement in and out of plots may also be critical (Kennedy and Way 1979). Relative to many pests' mobilities, the 80-315 m^2 plots used in this study were not large; they were, however, typical of the small, scattered fields planted by local farmers. Greater differences in the frequency of plant hosts may also be necessary to initiate pest resistance and stabilization mechanisms that are related to spatial diversity and resource concentration. Pimentel (1961 a,b) and Root (1973) both varied host densities over a wider range than in this study, but reached conflicting conclusions regarding the effects of diversity.

CHAPTER SIX
RESOURCE USE

Introduction

Amount and distribution of leaves and roots; soil moisture; and response to fertilization and watering were measured in the experimental systems as indicators of light, water, and nutrient use. Efficiency of use of these resources is defined, evaluated quantitatively where possible, and discussed. Mechanisms leading to improved resource use in intercrops are also discussed, including spatial partitioning of leaves and roots, differing resource response curves, compensatory growth, and temporal partitioning of growth.

Efficiency of use of human labor, a critical resource in Tanzanian agriculture, is also calculated and discussed.

Light, Water, and Nutrient Use

Results

Amount and vertical distribution of LAI

Leaf Area Index (LAI) was consistently higher in intercrops than in corresponding monocultures, as indicated by YERs greater than one calculated on the basis of LAI in both study years.

Leaf area distribution in the intercrop systems was also vertically stratified by species (Figures 105 and 106). Cowpea and pumpkin LAI were

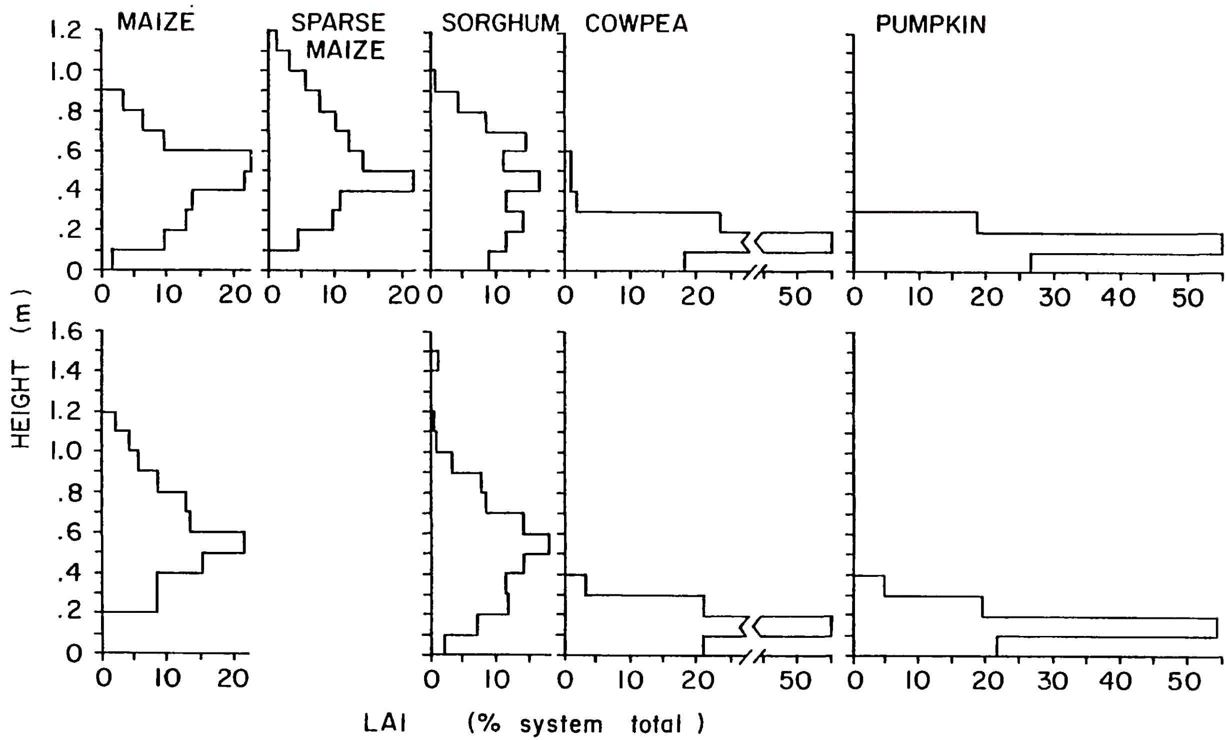

Figure 105. Vertical distribution of LAI in monoculture systems in the control treatment, Years 1 and 2. Data are from sample 2 in both years. The data are given as percent total LAI to facilitate comparison of curve shapes.

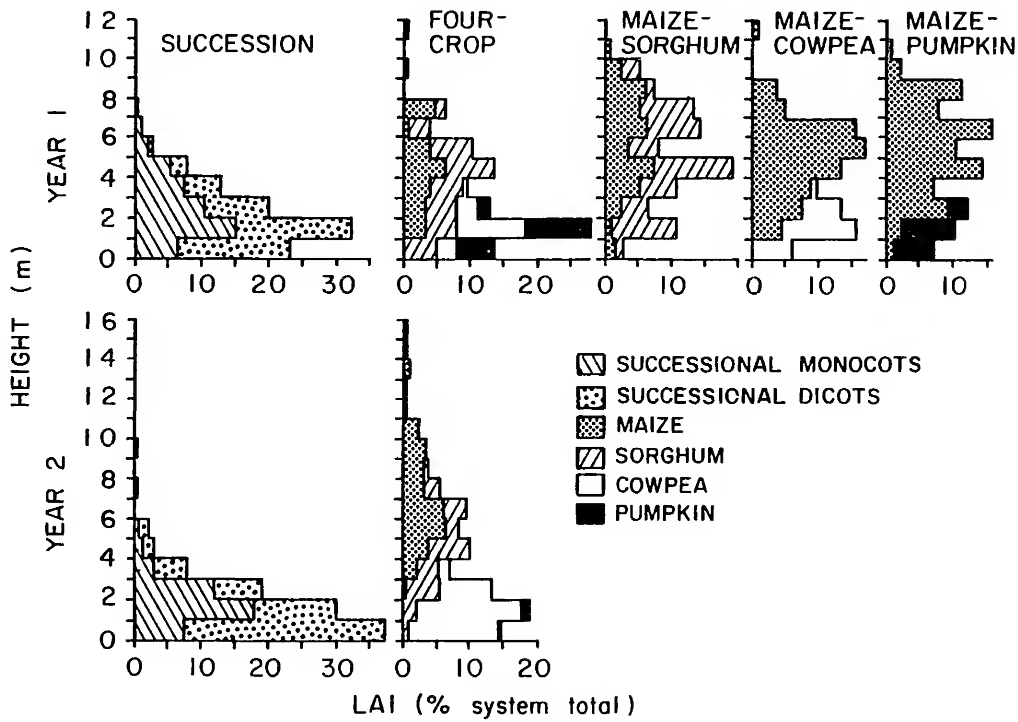

Figure 106. Vertical distribution of LAI in succession and intercrop systems in the control treatment, Years 1 and 2. Data are from sample 2 in both years. The data are given as percent total LAI to facilitate comparison of curve shapes.

concentrated in the 0-0.3 m height interval, whereas sorghum and maize LAI reached the heights of 0.9-1.5 m, with maxima from 0.4-0.6 m. Sorghum tended to have more leaf area just above the ground surface (0-0.2 m) than did maize. In the four-crop and maize-sorghum systems the tendency for maize to occupy a slightly higher zone was more pronounced. Leaf Area Index in the sparse maize monoculture (Year 1) was shifted slightly upward from that of the normal density maize monoculture; maize leaf area was also shifted slightly upward in the intercrop systems compared to maize monoculture in both years. Distribution of total LAI in the four-crop system was the most like that of the succession system in both years.

The fertilization and pesticide treatments had little effect on the vertical distribution of LAI in the sorghum, cowpea, and pumpkin monocultures, although a slight upward shift occurred with fertilization. Fertilization caused greater changes in the maize monoculture, four-crop, and succession systems (Figure 107). (LAI distribution in the pesticide treatment was approximately the same as that of controls in those three systems, and is omitted from the figure.) Fertilization of successional vegetation caused an upward shift of both monocot and dicot LAI, but the shift was more pronounced for monocots than for dicots. Monocot LAI was shifted upward with fertilization in the four-crop system, but dicot distribution remained unchanged. Maize and sorghum both occupied higher strata under fertilization than in the control treatment, but fertilization increased the vertical separation of the two species.

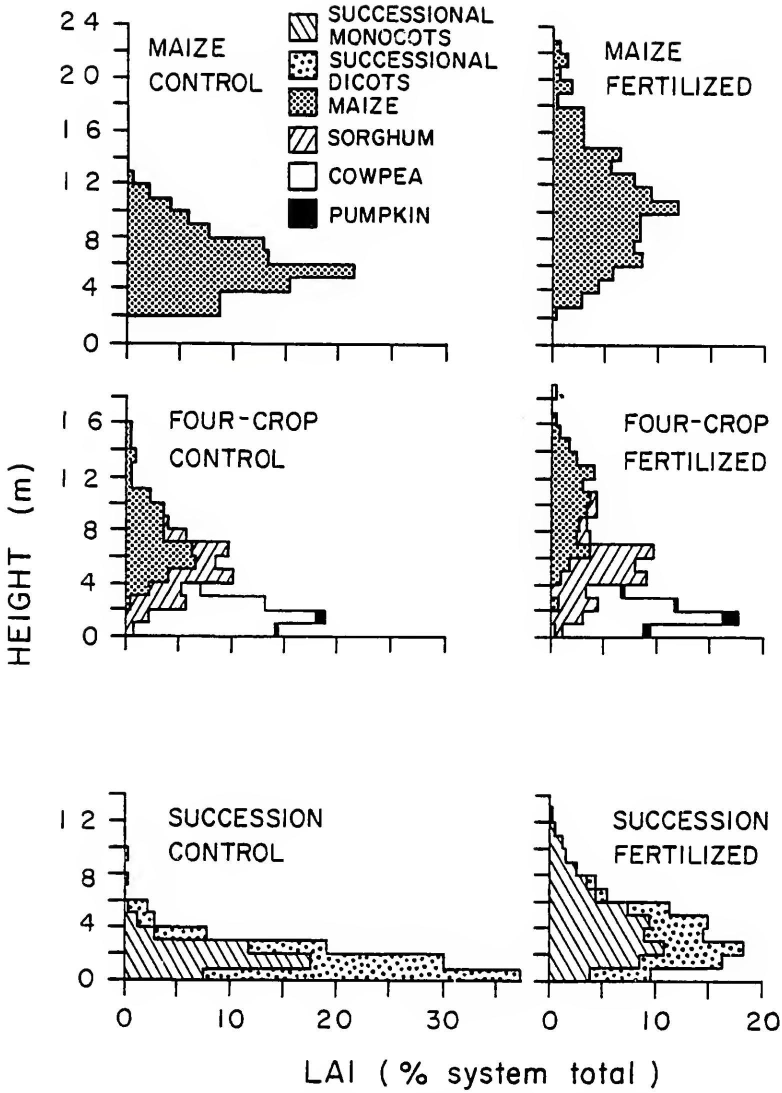

Figure 107. Vertical distribution of LAI in maize, succession, and four-crop systems, control and fertilized treatments, Year 2. Data are from sample 2. The data are given as percent total LAI to facilitate comparison of curve shapes.

Amount and vertical distribution of roots

Root biomass tended to be greater in intercrops than monocultures, as indicated by system YERs greater than one calculated on the basis of root biomass in both study years (Table 14). Year 2 data were generally more reliable than Year 1 data due to improved sampling methods.

Some differences in vertical distribution of roots, as well as root biomass, were also found among systems (Figure 108). Residual roots from previous vegetation were distributed uniformly to a depth of 40 cm, with a slight peak in the 10-20 cm depth interval. Roots in successional vegetation were also evenly distributed by depth. Nearly all roots were located in the top 10 cm of the soil profile in the maize, sparse maize, and four-crop systems, although the four-crop system had a much greater quantity of roots than the two maize monocultures. Sorghum monoculture had few roots in the top 30 cm of the soil profile, but deeper roots (30-40 cm) were found in both the sorghum monoculture and the maize-sorghum intercrop (and a few in the four-crop system). Pumpkin root biomass was low throughout the soil profile, but the maize-pumpkin system had root development comparable to that of the successional vegetation: well distributed and with maximum biomass in the top 10 cm. Roots were also relatively abundant and evenly distributed in the cowpea monoculture, but were less abundant and concentrated in the top of the soil profile in the maize-cowpea system.

Soil moisture

Soil moisture by the gravimetric method (used in Year 2 only) increased slightly (15-30 cm depth) in all systems during the first

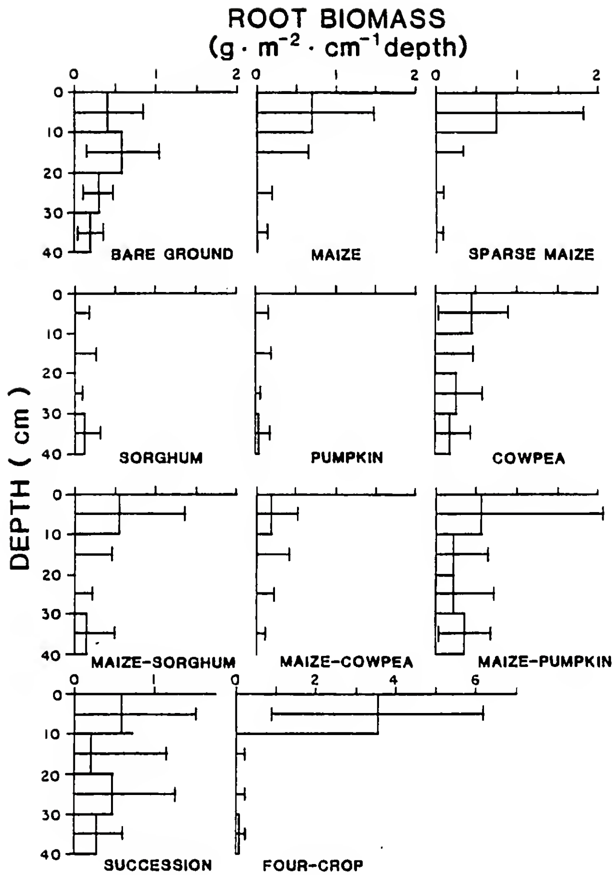

Figure 108. Vertical distribution of root biomass, Year 1. Root biomass in bare ground plots was subtracted in each depth interval from all other systems to correct for residual roots from the previous vegetation. Some slightly negative biomass values resulted from the corrections, and are graphed as zero.

part of the growing season to a maximum of 25-28 percent dry weight at day 85, then declined sharply, corresponding with cessation of rainfall and crop maturation (Figure 109). ANOVAs for system and treatment differences performed for each 10-day interval gave few consistent or significant differences. Soil moisture varied significantly among systems in the day 30-40 and day 100-110 intervals. The first of these was disregarded since the significance level was not high and the ordering of systems did not represent a consistent trend during adjacent sampling intervals. In the day 100-110 interval, cowpea soil moisture was approximately 4.5 percent higher than that of the other systems. Soil moisture was higher in cowpeas than in any other system in three of the last four sampling periods.

Soil moisture was significantly different among the control, fertilization, pesticide, and defoliation treatments (Figure 110) in the three sampling periods following day 90. In all three intervals, soil moisture was 1.2-3.2 percent lower in the control treatment than in the fertilization, pesticide, and defoliation treatments. The reason for this trend was not clear.

Discussion

Efficiency of total resource use

Efficiency is usually defined as output/input, although the point at which input and output are measured should be specified to avoid confusion (Kozlovsky 1968). In this study, diverse cropping systems produced more biomass than corresponding monocultures and successional

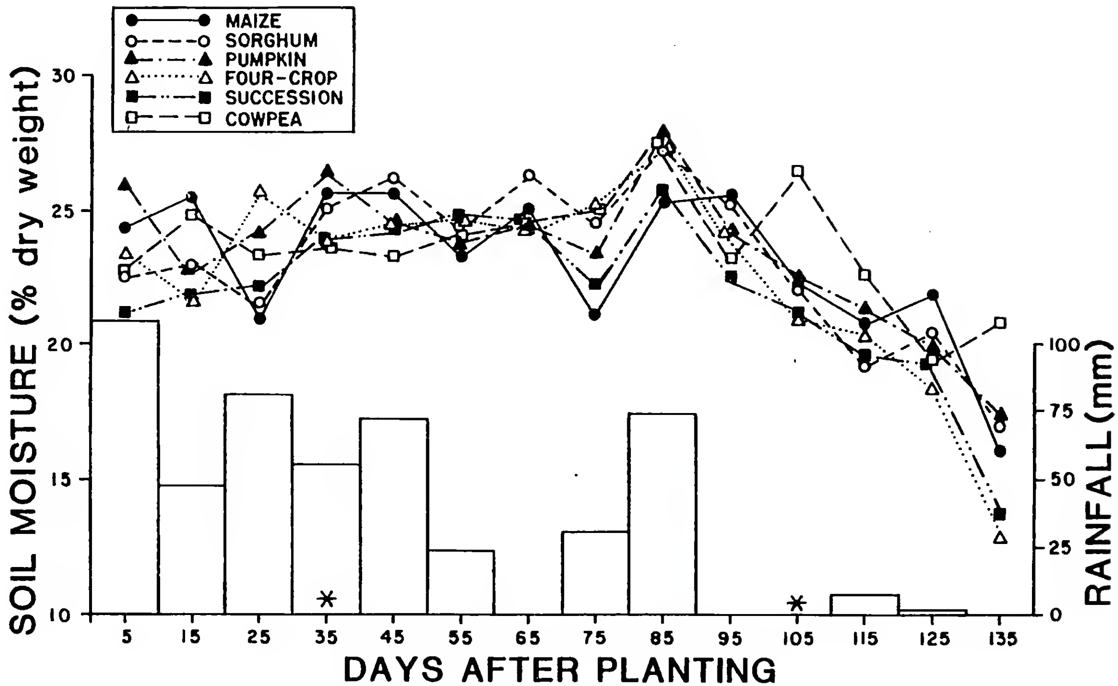

Figure 109. Soil moisture by time and system, Year 2. Each point is the mean of 1-30 (mean=14) determinations from all treatments combined, taken during a 10-day interval (graphed at mid-interval). ANOVAs gave significant differences among systems for intervals marked with asterisks. A rainfall histogram (by 10-day intervals) is given below the soil moisture graph.

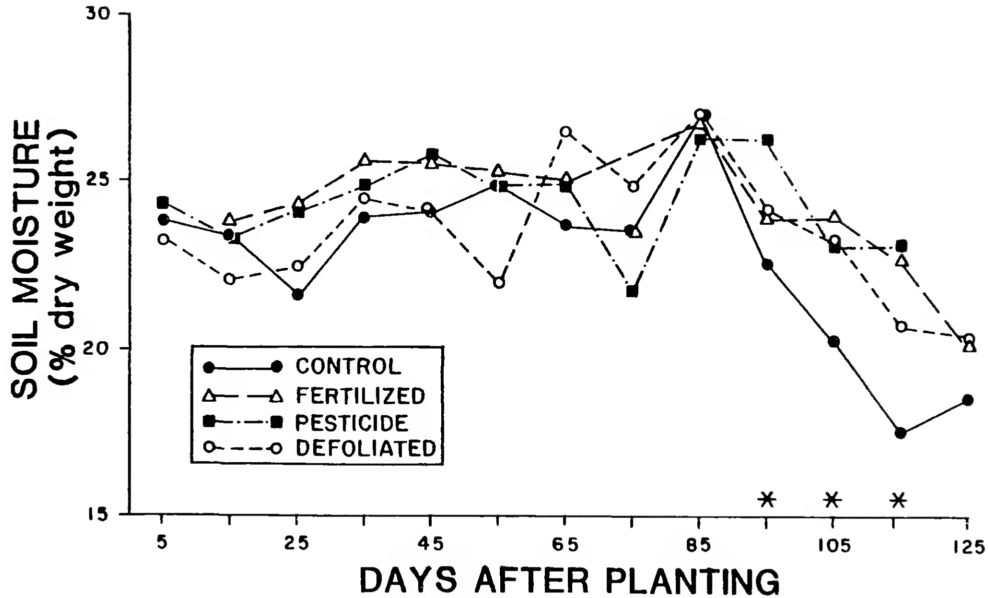

Figure 110. Soil moisture by time in four treatments, Year 2. Each point is the mean of 4-44 (mean=19) determinations from all systems combined, taken during a 10-day interval (graphed at midinterval). ANOVAs gave significant differences among treatments for intervals marked with asterisks.

vegetation produced the most biomass, with the same supplies of naturally occurring resources (light, water, and nutrients). Greater efficiency of total resource use in the succession and intercrop systems than in monocultures can then be inferred in terms of biomass output/available resources. Determination of the efficiency with which specific resources were used, and that in terms of resource uptake rather than resource availability, is much more difficult.

LAI and light use

Leaf Area Index was almost certainly suboptimal for maximum net primary productivity in all systems and treatments in this study (see Evans 1975). At suboptimal LAI, net productivity per unit ground area (biomass output/total radiation) and efficiency of light interception (light intercepted/total radiation) should increase with increasing LAI, but photosynthetic efficiency (biomass output/radiation intercepted) should decrease with increasing LAI. The slightly higher LAI and canopy cover in intercrops than in corresponding monocultures therefore implies greater light use efficiency (output/total radiation). It is doubtful, however, that the slight increases in LAI in intercrops could account entirely for the large differences found in productivity.

Distribution of leaf angles and of sun- and shade-adapted leaves throughout the canopy may have greater effects on productivity than LAI. Trenbath (1977) has shown using models that light utilization is improved when leaves with shallow leaf angles (near horizontal) are located near the bottom of the canopy and more vertical leaves are located near the top of the canopy, compared with the same LAI of

randomly distributed leaf angles. Leaf angles were not measured in this study, but cowpea and pumpkin leaves are obviously more nearly horizontal than maize and sorghum leaves, and were found to occupy a lower portion of the canopy than maize and sorghum. Light utilization may also be improved by microclimatic effect on understory species, especially if those species are shade-adapted. Placement of shade species in the lower portion of the canopy and sun species in the top of the canopy should increase total system productivity, even if the shade species' productivity is depressed by low light levels. Maize and sorghum are known to have high productivity response to radiation. Both are sun-adapted, C-4 species (Evans 1975, Milthorpe and Moorby 1975). Cowpea and pumpkin are C-3 species and are presumably more tolerant of shaded conditions and have lower optimum leaf temperatures.

Leaf Area Index was highest in the succession system (indicating high light interception), and vertical distribution of successional monocots and dicots very nearly matched that of agronomic monocots and dicots in the four-crop system. Biomass productivity per unit LAI, however, was greatest in the intercrop systems and maize and sorghum monocultures (Table 73). This was probably due to shading effects within the successional vegetation canopy (as expected when optimum LAI is approached), and to early maturation of successional species. Lower biomass productivity per unit LAI in succession may also reflect the use of photosynthetic energy for biochemical or structural adaptations that do not show up as biomass accretion. Agronomic species, on the other hand, have been selected for high edible biomass productivity, presumably at the expense of structural or biochemical adaptations that do not contribute to edible yield.

Table 73. Efficiency of light utilization as biomass productivity/LAI, Years 1 and 2. Data are from control plots only. Year 2 LAI was the second sample (day 65); Year 1 LAI was linearly interpolated to day 65. Efficiencies are g total biomass at harvest/m^2 leaf, and do not take into account leaf turnover.

	EFFICIENCY		RANK	
SYSTEM	YEAR 1	YEAR 2	YEAR 1	YEAR 2
MAIZE	307.4	451.8	3	3
SORGHUM	384.1	482.2	2	2
COWPEA	23.8	74.1	6	6
PUMPKIN	151.6	133.3	5	5
SUCCESSION	159.8	193.6	4	4
FOUR-CROP	465.3	786.1	1	1
CORRESPONDING MONOCULTURES	249.3	347.9		
MAIZE-SORGHUM	334.0			
CORRESPONDING MONOCULTURES	349.4			
MAIZE-COWPEA	384.2			
CORRESPONDING MONOCULTURES	208.9			
MAIZE-PUMPKIN	337.6			
CORRESPONDING MONOCULTURES	257.4			

Biomass production per unit leaf area was distinctly higher in all intercrop systems except maize-sorghum than in corresponding monocultures (Table 73). This finding lends support to the idea of increased productivity due to improved light utilization (rather than just increased LAI) in mixtures. The low difference in efficiency between the maize-sorghum intercrop and corresponding monocultures might well be because of similarities in maize and sorghum canopy structure and photosynthetic pathways. Alternatively, increased productivity/LAI in intercrops could result from improved use of resources other than light.

Root biomass amount and distribution: use of soil resources

Increased root biomass and dispersed rooting throughout the soil volume (due to spatial partitioning of root zones) should result in increased nutrient and water uptake in intercrops, and hence greater resource use efficiency in terms of biomass production/resources available. Results from this study showing greater root production in intercrops than monocultures and correlation of root biomass with productivity lend support to this statement, but it is not clear whether increased rooting caused productivity increases or the opposite.

The Year 1 root profiles lend support to the idea of spatial partitioning in the rooting zone, but the results are not conclusive due to high variability among samples. Sorghum roots tended to be deeper than maize roots, pumpkin roots tended to be shallow, and roots were most evenly distributed (vertically) in the succession system. Root zone partitioning has been shown to occur by many other researchers (see Introduction), but it has not been directly experimentally linked to nutrient and water use.

Even distribution of roots through the soil volume (both vertically and horizontally) should increase nutrient and water uptake of a system, even for systems of equal root biomass. Soil water and nutrients would be extracted evenly, so the probability of a given plant experiencing water or nutrient stress would be reduced. A more clumped distribution of the same root biomass would be more likely to create local nutrient and water deficits.

Complementary moisture and nutrient response

Mixing of crops with different moisture or nutrient response curves ("requirements") should also reduce competition and increase biomass productivity/resources available, independent of differences in root biomass. In such a mixture, productivity of the species with high water or nutrient requirements would increase due to reduced competition. (Interspecific competition by a neighbor with low requirements would be less than intraspecific competition.) The productivity of the second species would be only slightly adversely affected by neighbors having high resource demand, since it is tolerant of low resource levels. Intercrop yield of such a mixture should exceed that of corresponding monocultures.

Maize and sorghum are an example of species having complementary moisture response curves; maize is unstable with respect to both excessive and insufficient moisture, whereas sorghum gives reliable yields over a wide range of conditions (Glover 1948, Glover 1959, Doggett and Jowett 1966). Complementarity of nutrient requirements is also very likely to be occurring, especially in mixtures containing nitrogen fixing legumes.

The high YER of maize in the maize-cowpea system was probably largely due to such complementarity.

Efficiency of nutrient use

Nutrient uptake in the crop systems was not directly determined, but if the available nutrient pool is assumed to be a constant, biomass output/nutrients available was higher in intercrops than in corresponding monocultures. Use of the total nutrient pool in the fertilization treatment was also more efficient in intercrop than monoculture. The nutrients added in the fertilized treatment were used with the same efficiency in the four-crop intercrop and corresponding monocultures, however, as indicated by equal increases in LAI and biomass in response to fertilization. Added nutrients were used most efficiently in the maize, succession, and sorghum systems. The response of successional aboveground biomass, but not root biomass, to fertilization suggests that the succession system was closer to fully exploiting soil resources in unfertilized conditions than were the agronomic systems.

Numerous other studies have shown greater nutrient uptake in intercrops than monocultures, as well as greater soil fertility following intercrops than monocultures (see review by Kass 1978). These studies are difficult to interpret, however, for several reasons. First, planting density of intercrops may not equal that of monocultures; if planting density is higher than that of monocultures, it is rather likely that greater nutrient uptake in the intercrop is due at least partly to increased plant density, rather than increased diversity. Second, nutrient uptake or soil nutrient depletion in intercrops is

very often compared with that of one or both monocultures, rather than a weighted mean of monocultures. Comparisons of maize-legume intercrops with maize monoculture are common but are particularly difficult to interpret. Third, the role of legumes in intercrop nutrient budgets has still not been clarified. Nitrogen fixation may be responsible for seemingly conflicting results that show both higher nutrient content and higher levels of residual soil nutrients in intercrops. Fourth, the effects of rooting volume and spatial distribution of roots are poorly understood. Even distribution of roots through a large soil volume may simultaneously increase nutrient uptake and prevent leaching of residual nutrients more effectively than a patchier distribution of the same root biomass. Finally, even if greater nutrient uptake in intercrops is shown, feedback between above- and belowground parts makes it impossible to say whether such differences are the cause or effect of productivity differences. The issue of nutrient use is clearly a very complex one that needs further detailed study.

Efficiency of water use

Water use efficiency has been defined as biomass accumulation per unit of water transpired (Fischer and Turner 1978). In arid areas, systems having efficient water use tend to have a higher ratio of water transpired to water evaporated from the soil surface than systems of low water use efficiency. High transpiration and low surface evaporation are both functions of LAI, so one can generalize that high LAI and high water use efficiency go hand-in-hand in arid areas (Fischer and Turner 1978). By this reasoning the higher LAI of the intercrop systems in this study would imply efficient water use.

Soil moisture levels did not vary significantly among systems in this study (except on one date, which may be attributed to experimental error). Water use efficiency would then seem to be higher in the intercrops due to their higher productivity. Another possibility is that water uptake was greater in the intercrop systems than in monocultures (as suggested by their higher LAIs), but that soil moisture was held at approximately field capacity by frequent rains. The low response of all crops to the watering treatments shows that water was not limiting during the study, and is consistent with that interpretation. Even if soil moisture is near field capacity throughout the growing season, partial shading of understory plants could prevent midday loss of turgor due to high transpiration rates (Trenbath 1974), thereby increasing water use efficiency compared with monocultures.

Kass (1978) reviewed several studies in which water use in intercrops and monocultures were directly monitored, but the results were inconclusive and, once more, confounded by differing overall planting densities.

Compensation

In addition to spatial partitioning of leaves and roots and differing factor-response curves, compensatory growth and temporal partitioning of resource use may contribute to improved resource use and increased productivity in mixtures (Trenbath 1974). Compensation may be thought of as the reverse of competitive inhibition; competitive inhibition is the suppression of one species by growth of another species (by way of mutually limiting resources), whereas compensation

is stimulation of one species by loss of another (mediated again through levels of limiting resources). Resource partitioning, compensation, and competitive inhibition all produce differing growth rates among species. Controlled plant-removal experiments are the only way to conclusively determine that a species' productivity has increased due to reduced vigor of a neighbor.

Two factors that determine the degree of compensatory growth are the types and amounts of resources released (e.g., increased light to the understory with removal of overstory plants, but not the reverse), and the genetic ability of another species to respond to those changes with increased growth. Both factors appeared to be operating in a maize-peanut intercrop in which peanut responded positively to maize removal, but maize did not compensate for peanut removal (Liboon et al. 1976). Mixing of crops with different response curves should enhance a system's capacity for compensatory growth. A drought- or flooding-tolerant species, for example, may compensate for loss of a sensitive species early in the growing season; intercrop yield should exceed that of corresponding monocultures. Sorghum may be able to compensate for loss of maize due to moisture stress early in the growing season. Whether compensation can occur in the grain-filling stage in response to end-of-season water shortages is still an open question. Species with low nutrient requirements, similarly, may compensate for low productivity of high-nutrient-demand species under conditions of nutrient stress.

Negative correlation between the productivity of two system components suggests compensatory growth, but does not prove it. Compensation can occur between two species that covary positively over

a range of resource levels, and a negative correlation of two species' productivities may be due to factors other than compensation, such as changes in environmental factors that favor one species but not the other. In the latter case it is very likely that differential growth of the two species would cause a further release of resources that would cause compensatory growth. Direct effects of an externally originating change in a resource and an internally originating change due to differential growth rates and competition among species, are virtually impossible to distinguish without plant removal experiments. Such experiments cannot, however, reveal the extent to which compensatory growth occurs under natural environmental fluctuations.

In this study, productivity of maize, sorghum, and pumpkin covaried positively over a range of conditions (the Year 2 stress treatments, Table 74). These relationships held even when fertilized plots were removed from the analysis; fertilization caused sizable increases in all species' productivity and thus, positive covariation. Cowpea productivity was weakly negatively correlated with that of maize and pumpkin. This negative relation may have been due to simultaneous stimulation of cowpea and suppression of maize and pumpkin by the pesticide treatment, but it is likely that compensatory growth of cowpeas in plots in which pumpkin and maize were unproductive also occurred.

Successional monocot and dicot productivity also tended to be slightly negatively correlated, especially in terms of root growth. This may have been due to competitive inhibition of dicots by monocots rather than compensatory growth (especially in fertilized plots). Compensation by dicots for loss of monocot leaf area in the defoliation

Table 74. Interactions between pairs of crops in the four-crop system and between successional monocots and dicots, Year 2. Values are Pearson product-moment correlation coefficients for all treatments combined (first line) and all treatments except fertilization (second line).

INTERACTING SPECIES PAIR	BIOMASS[a]	BIOMASS[b]	EDIBLE BIOMASS[a]	ROOTS[b]	LAI[b]	LAI[c]	FULLSTAND-EDNESS[d]	OVERALL INTERACTION
MAIZE-SORGHUM	.72‡ .66‡	.72‡ .83†	.25 .60‡	.81‡ .66	.69† .72	.49 .08	-.01 -.03	Strong Positive
MAIZE-COWPEA	.06 -.10	.13 .10	-.43† -.33	.33 .78	.01 -.08	-.17 -.06	.21 .24	Weak Negative
MAIZE-PUMPKIN	.63‡ .71‡	.18 .89†	-- --	.10 .20	.20 .78	.55† .57	.46† .49†	Strong Positive
SORGHUM-COWPEA	.26 .26	.34 .20	.11 .10	.61† .59	.28 .10	.06 .62†	-.01 -.04	Weak Positive
SORGHUM-PUMPKIN	.58‡ .75‡	.43 .53	-- --	.14 .18	.45 .36	.72‡ .17	.29 .33	Strong Positive
COWPEA-PUMPKIN	-.16 -.16	-.15 .25	-- --	-.27 .04	-.17 .25	-.26 -.28	.15 .37	Weak Negative
SUCCESSIONAL MONOCOTS-DICOTS	-.13 -.08	.38 -.41	-- --	-.30 -.48	-- --	.22 -.16	-- --	Weak Negative
n =	24-25 19-20	10-11 5-6	24 19	11 6	11 6	16 11	24 19	

[a] at harvest
[b] at flowering
[c] second LAI sample
[d] third stand count
† significant at $p < .05$
‡ significant at $p < .01$

treatment was probably occurring, however. Suppression of dicots by monocots under fertilization, and compensation by dicots for loss of monocots with defoliation have also been shown by Donald (1963) in mixed pastures.

It is likely that the intercrop advantage consistently found in this study was largely due to compensatory growth by maize and sorghum in response to the high mortality of cowpea and pumpkin. Pest and disease attack to the two dicot species constituted a natural "plant-removal" experiment. Unfortunately, the necessary control (full-productivity cowpea and pumpkin populations) was missing, so the effect of compensatory growth could not be distinguished from that of other mechanisms that improve resource use in intercrops.

Temporal partitioning

Temporal partitioning of growth is a mechanism for improved resource use that operates much as compensatory growth does. Reduced growth of one species at one time releases resources for increased growth of a second species; the relationship is reversed at a later time. Staggered LAI development curves have been suggested as evidence of temporal partitioning of growth processes in general (Kassam and Stockinger 1973).

The shape of LAI and length curves in this study suggests that temporal partitioning of resources occurs in the four-crop system; the effect on system productivity should be positive. Sorghum length and LAI development weremore rapid than those of maize in the middle of the growing season, but slower at the end of the season. Also, cowpea and

pumpkin continued to elongate late in the growing season, but leaf area was constant or declined at the end of the season, probably due to high rates of leaf turnover (death and decomposition of leaves). Nevertheless, increased percent monocot LAI later in the growing season and the continued elongation of dicots suggest both greater utilization of above- and belowground resources by monocots relative to dicots (a form of temporal partitioning). and high capacity for compensatory growth by dicots during the last half of the growing season. In successional vegetation, in contrast, patterns of temporal development of LAI were the same in monocots and dicots. (Percent monocot LAI was constant.)

Human Labor Use

Human labor may be the resource that most limits productivity in rural Tanzania, where marginally arable land is relatively abundant but the labor supply is limited. In more populated areas, and on more productive soils, efficient use of land rather than labor may be the most important factor limiting per capita production. The critical nature of the labor resource has been accentuated in Tanzania by the recent enactment of universal primary school education, which has greatly reduced the role of children in the agricultural labor force.

Results

In both study years, maize and pumpkin monocultures used the least planting labor, while the sorghum, four-crop, and cowpea systems tended to have high labor requirements (Figure 111). In Year 2,

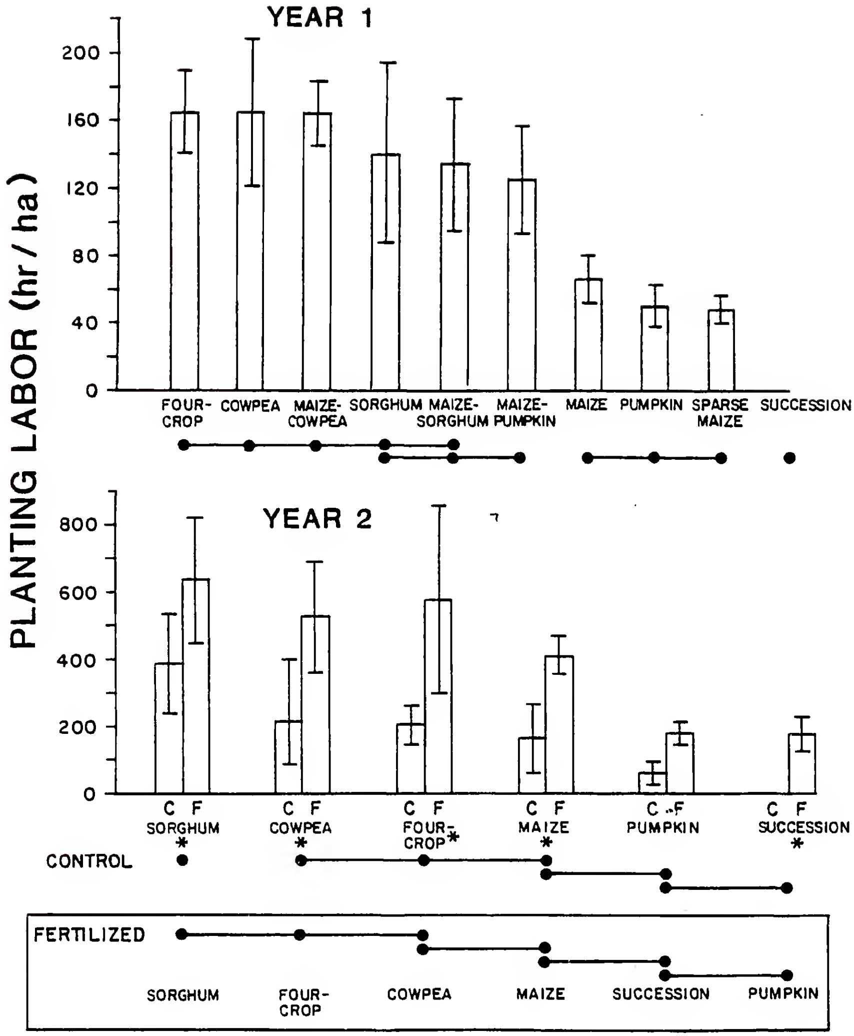

Figure 111. Planting labor, Years 1 and 2. Year 1 data are from the control treatment; Year 2 data are from the control and fertilized treatments (C and F, respectively). Systems not sharing a common line are significantly different by Duncan's tests, performed separately for the two treatments in Year 2. Asterisks indicate significant differences between the control and fertilized treatments in Year 2.

application of fertilizer at planting significantly increased planting labor in all systems except pumpkin monoculture.

Planting labor was significantly higher in all intercrop systems than in corresponding monocultures in Year 1 (Figure 112). In Year 2, planting labor was significantly higher in the four-crop system than in corresponding monocultures when tested for a sample of the control and fertilization treatments combined, but the intercrop/monoculture difference was negligible in the control treatment. Planting labor was highly correlated with planting density regardless of the species planted (r = .66 in Year 1, r = .99 and .90 in Year 2 control and fertilized plots, excluding data from the succession system).

Labor use during the first weeding was greatest in the sorghum and cowpea systems and lowest in the pumpkin and maize-pumpkin systems in Year 1. In the second weeding, the sorghum system again required the most, and pumpkin monoculture the least, weeding labor; cowpea weeding labor was also very low (Figure 113). In Year 2, pumpkin weeding time was again consistently low; sorghum and cowpea had the highest weeding time in the first weeding, but the four-crop system was highest in the second weeding (Figure 114). Weeding times in Year 2 were more than double those in Year 1 due to increased weed growth. The only significant effect of the stress treatments on weeding time (compared to controls) in Year 2 was significantly reduced weeding time in the pesticide-sprayed plots.

Weeding labor in the four-crop intercrop was significantly greater than that of a mixture of corresponding monocultures in the second weeding in Year 2 (Figure 115); all other intercrop/monoculture differences

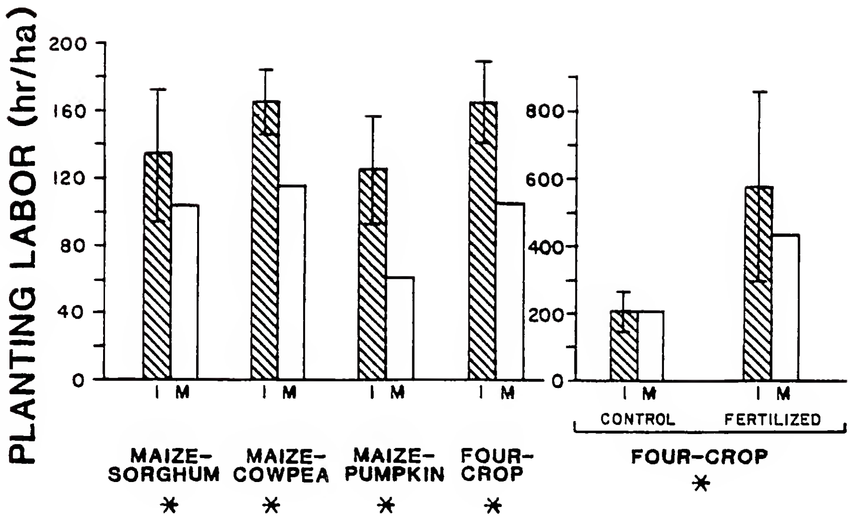

Figure 112. Comparison of planting labor in intercrops and corresponding monocultures, Years 1 and 2. I = intercrop (hatched bars); M = monocultures (open bars). Asterisks indicate significant differences between intercrop and monoculture systems by SAS Contrast procedure, performed on samples of the control and fertilized treatments combined in Year 2.

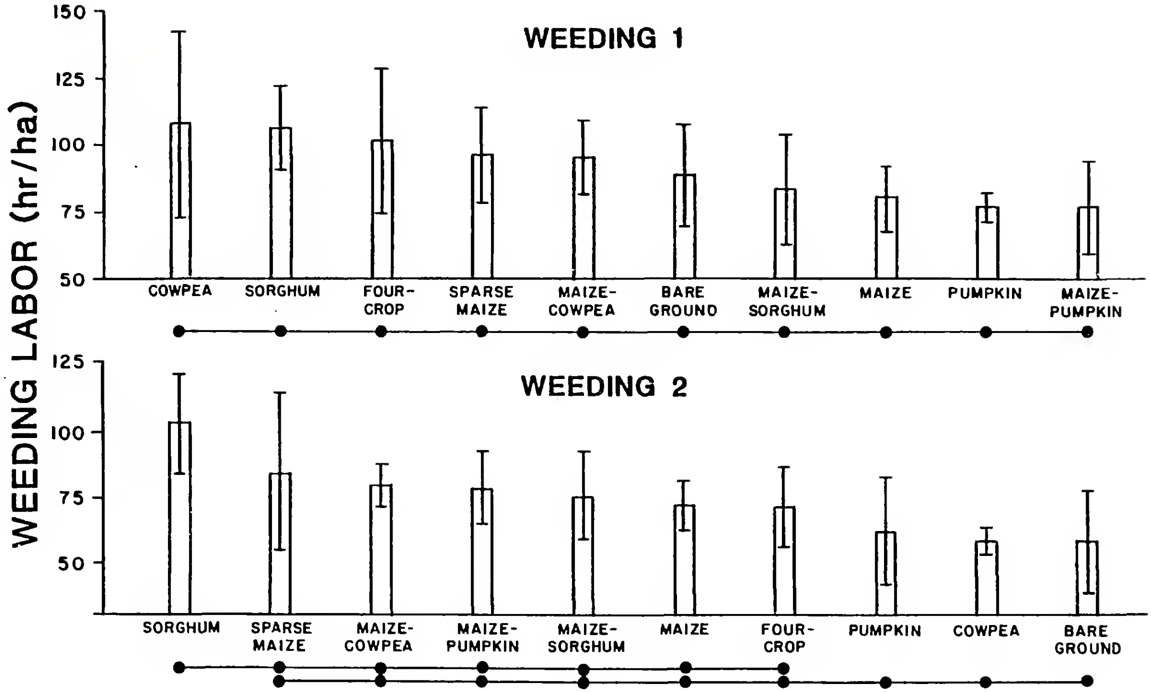

Figure 113. Weeding labor, Year 1. Systems not connected by a common line are significantly different by Duncan's tests.

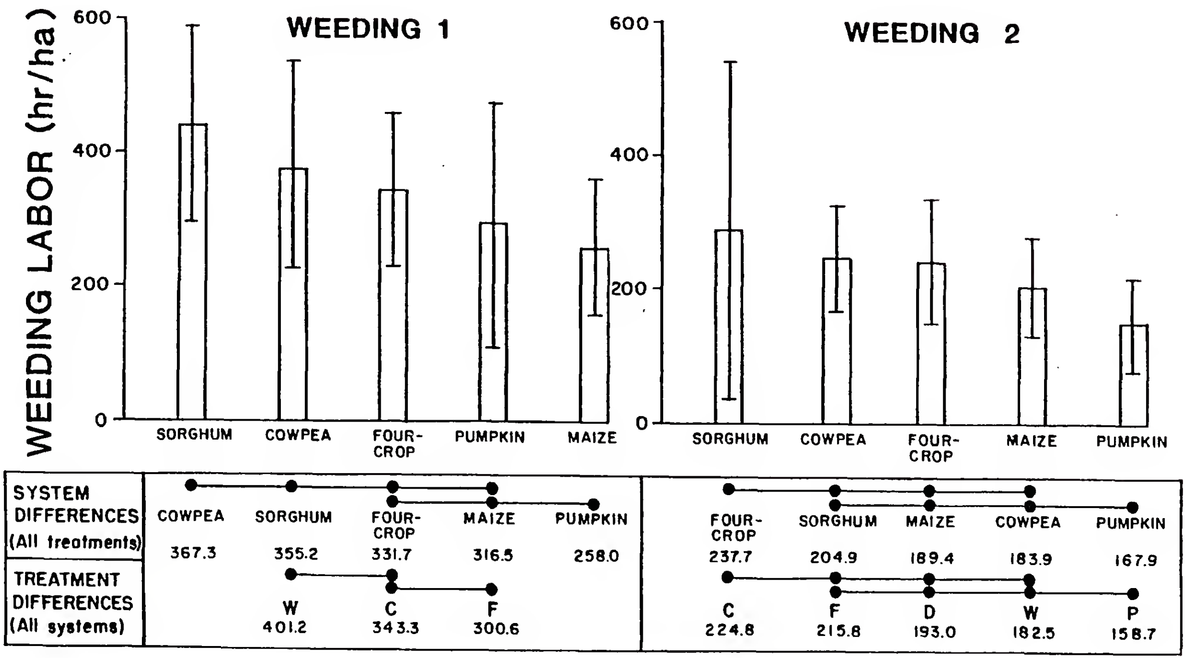

Figure 114. Weeding labor, Year 2. Histograms are based on control treatment data. Systems or treatments not connected by a common line are significantly different by Duncan's tests, performed on samples of all treatments or systems combined. (Mean weeding labor for those samples is given with the Duncan's tests.) C = control treatment, F = fertilized, P = pesticide, D = defoliated, W = watered. Pesticide and watered treatments were deleted from the first weeding data because the treatments had not yet had time to take effect.

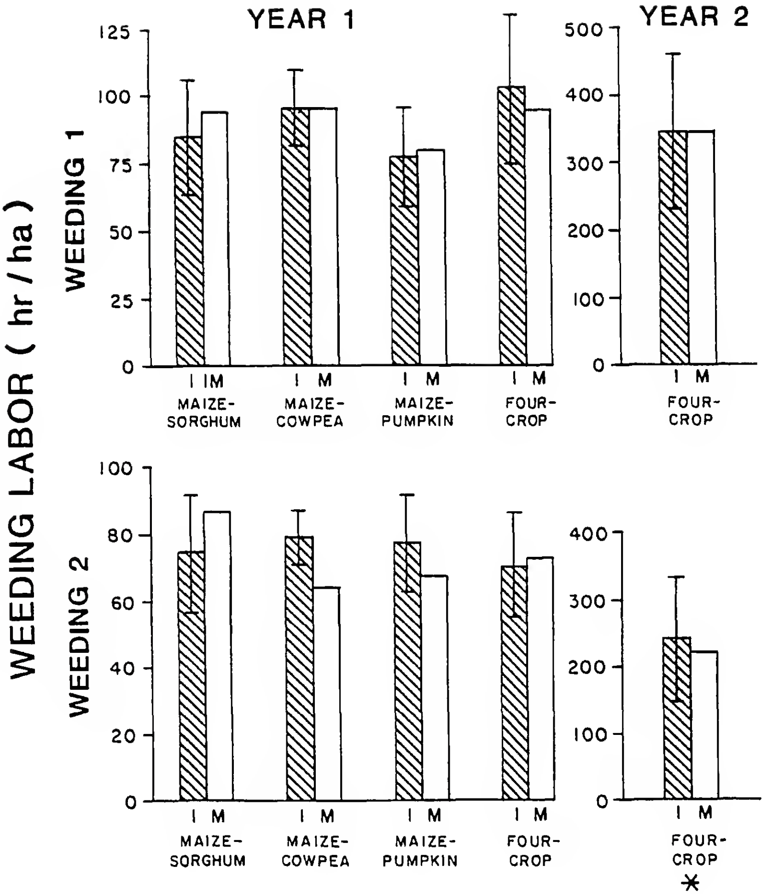

Figure 115. Comparisons of weeding labor in intercrops and corresponding monocultures, Years 1 and 2. I = intercrop (hatched bars); M = monoculture (open bars). Significant intercrop/monoculture differences are indicated with an asterisk (SAS Contrast procedure, performed on samples of all treatments combined in Year 2).

were nonsignificant. The increased labor use in the four-crop compared with corresponding monocultures was especially evident in the fertilized treatment.

Weeding labor was highly correlated with planting density in samples of all systems combined (r = .67 and .52 in Year 1 first and second weedings, r = .88 and .98 in Year 2 control plot first and second weedings).

Labor use efficiency

Labor use efficiency (edible or total output/labor input) may be a more meaningful measure than hr/ha required for various agronomic activities (Tables 75 and 76). In Year 2 the most labor-efficient system (in terms of planting labor, weeding labor, and planting plus weeding labor) was maize monoculture. In Year 1 the three two-crop intercrops and sparse maize were more efficient than maize monoculture in terms of planting labor, but only sparse maize had greater weeding labor efficiency, presumably because of the low density of plants. On an absolute scale, the four-crop, cowpea and pumpkin systems tended to have low labor use efficiencies in both years with a few exceptions. The higher edible yield of maize with respect to total labor (Year 2) and weeding labor (Year 1) is probably a major reason for its current popularity in Tanzania.

Efficiency of weeding and total labor use was higher in intercrops than corresponding monocultures; planting labor efficiency was approximately the same in intercrops and corresponding monocultures (Table 77).

Efficiency of labor use was consistently greater in fertilized than control plots with respect to all labor variables (planting, weeding, total) and assessed in terms of either edible or total yield.

Table 75. Labor use efficiency among systems, Year 1. Values are kg edible and total yield/hr labor; rankings of the systems by efficiency are given below the means in parentheses. Data are from control plots only. Planting labor was measured in the small plots and weeding labor in the main plots, so total labor use efficiency was not calculated. Weeding labor = weeding 1 + weeding 2.

	MAIZE-SORGHUM	MAIZE-PUMPKIN	MAIZE-COWPEA	SPARSE MAIZE	MAIZE	SORGHUM	FOUR-CROP	COWPEA	PUMPKIN
PLANTING LABOR									
EDIBLE YIELD	7.47 (1)	6.92 (2)	6.54 (3)	6.11 (4)	5.99 (5)	4.43 (6)	4.41 (7)	.04 (8)	0 (9)
TOTAL YIELD	22.90 (1)	20.91 (2)	17.26 (4)	17.39 (3)	16.77 (5)	16.40 (6)	13.18 (7)	.59 (9)	8.13 (8)
WEEDING LABOR									
EDIBLE YIELD	5.62 (5)	5.17 (6)	6.38 (4)	15.21 (1)	8.58 (2)	7.31 (3)	4.02 (7)	.09 (8)	0 (9)
TOTAL YIELD	19.04 (6)	21.24 (4)	13.13 (7)	36.01 (1)	29.29 (2)	19.41 (5)	11.63 (8)	.53 (9)	25.24 (3)

Table 76. Labor use efficiency among systems, Year 2. Values are kg edible and total yield/hr labor. Rankings of the systems by efficiency are given below the means in parentheses. Data are from the control plots. Weeding labor = weeding 1 + weeding 2; total labor = planting labor + weeding labor.

	MAIZE	SORGHUM	FOUR-CROP	PUMPKIN	COWPEA
PLANTING LABOR					
EDIBLE YIELD	4.06 (1)	3.67 (4)	2.36 (3)	1.57 (2)	.29 (5)
TOTAL YIELD	16.57 (1)	10.57 (3)	10.07 (2)	7.05 (4)	2.95 (5)
WEEDING LABOR					
EDIBLE YIELD	2.02 (1)	1.17 (2)	1.17 (3)	1.17 (4)	.13 (5)
TOTAL YIELD	7.83 (1)	7.59 (2)	5.47 (3)	2.00 (4)	1.40 (5)
TOTAL LABOR					
EDIBLE YIELD	1.24 (1)	.81 (4)	.73 (3)	.61 (2)	.09 (5)
TOTAL YIELD	4.93 (1)	3.90 (2)	3.37 (3)	1.44 (4)	.88 (5)

Table 77. Labor use efficiency in intercrops and corresponding monocultures, Years 1 and 2. All data are from control plots. Weeding labor efficiencies (kg/hr labor) are based on weeding 1 + weeding 2 labor inputs; total labor efficiencies are based on planting labor + weeding labor, and exclude other important labor inputs such as thinning, harvesting, and processing. In Year 1, planting labor was measured in the small plots and weeding labor in the main plots, so total labor use efficiency was not calculated. Efficiences are also shown for corresponding monocultures of the intercrop systems (total yield/labor input).

	EFFICIENCY (kg/hr labor)					
	PLANTING LABOR		WEEDING LABOR		TOTAL LABOR	
SYSTEM	EDIBLE	TOTAL	EDIBLE	TOTAL	EDIBLE	TOTAL
YEAR 1						
MAIZE-SORGHUM	7.47	22.90	5.62	19.04		
CORRESPONDING MONOCULTURES	8.94	28.37	5.31	16.86		
MAIZE-COWPEA	6.54	17.26	6.38	13.13		
CORRESPONDING MONOCULTURES	3.44	12.80	2.79	10.39		
MAIZE-PUMPKIN	6.92	20.91	5.17	21.23		
CORRESPONDING MONOCULTURES	3.16	32.26	2.15	13.42		
FOUR-CROP	4.41	13.18	4.02	11.63		
CORRESPONDING MONOCULTURES	4.48	16.67	2.88	10.74		
YEAR 2						
FOUR-CROP	2.36	10.07	1.17	5.47	.73	3.37
CORRESPONDING MONOCULTURES	1.63	9.41	.58	3.36	.43	2.48

Discussion

Intercrop systems in this study were consistently more difficult to plant than corresponding monocultures (Table 78). This may have been due partly to the need to manipulate several planting ropes and bags of seed. Farmers in their own fields may plant intercrop systems faster than corresponding monocultures by dropping several kinds of seeds in the same hole. The potential of same-hole planting to reduce labor demand may be one reason that the practice is widespread, despite increased competition among crops. Weeding times should also be reduced by same-hole planting since weeding time and number of planting holes were highly correlated.

Date of planting is often critical in Tanzania. Same-hole planting of intercrop systems would allow greater areas to be planted, increasing the probability that a given minimum area would be planted during the most favorable period. Replanting could also be accomplished more quickly and labor freed for other (perhaps cash-crop) fields.

The maize-sorghum, maize-cowpea, and four-crop systems required less time to weed than corresponding monocultures in Year 1, but the maize-pumpkin and Year 2 four-crop systems took longer to weed than monocultures (Table 78). The hidden, crawling stems of pumpkin may have been responsible for the additional care required in those two systems, which were partially hand-weeded to avoid cutting the stems with hoes. Although intercrop systems often required more time to weed, this may be more than offset by reduced need to weed. Reduced weed growth was found in all intercrop systems except maize-pumpkin (Table 78), and may be a much more important feature of intercrop

Table 78. Summary of weed growth, labor use, and labor use efficiency in intercrops and corresponding monocultures, Years 1 and 2. Intercrop systems and their corresponding monocultures are ranked by each variable; 1 = lower value for weed biomass and labor use, 2 = higher value for labor use efficiency. Data are from control treatment plots.

	WEED GROWTH[a]	PLANTING LABOR USE	WEEDING LABOR USE[b]	PLANTING LABOR EFFICIENCY[c]	WEEDING LABOR EFFICIENCY[c]
YEAR 1					
MAIZE-SORGHUM	1	2	1	2	1
CORRESPONDING MONOCULTURES	2	1	2	1	2
MAIZE-COWPEA	1	2	1	1	1
CORRESPONDING MONOCULTURES	2	1	2	2	2
MAIZE-PUMPKIN	2	2	1	1	1
CORRESPONDING MONOCULTURES	1	1	2	2	2
FOUR-CROP	1	2	1	2	1
CORRESPONDING MONOCULTURES	2	1	2	1	2
YEAR 2					
FOUR-CROP	1	2	2	1	1
CORRESPONDING MONOCULTURES	2	1	1	2	2

[a]third weeding

[b]second weeding

[c]based on edible yield

systems than increased difficulty of weeding. Farmers tend to weed their fields when weed growth exceeds a certain level; suppression of weed growth should reduce the frequency of weeding and thereby substantially reduce weeding labor. If the farmer omits a weeding due to labor shortage, as often occurs, reduced weed growth should result in higher productivity in the intercrop systems.

Greater productivity in intercrops more than offset the increased difficulty of cultural operations in mixed fields. Efficiency of labor use in intercrops was consistently equal to or higher than that of corresponding monocultures. The same was true of fertilized plots of all systems, where increased productivity again resulted in high labor use efficiency. Kass's (1978) conclusion that benefits of intercropping are not clear with respect to labor would perhaps be different if based on analyses of efficiency rather than absolute amounts of labor use.

CHAPTER SEVEN
IMPLICATIONS FOR AGROECOSYSTEM DESIGN

Species Composition of Intercrop Systems

Choice of species and planting times in an intercrop system will determine the extent of its productivity and stability advantage compared with monocultures. Although the purpose of this study was not to determine morphological and physiological characteristics of crop species that are advantageous in intercrop systems, several species and system characteristics did appear to be associated with high system stability and/or productivity. Increased productivity in intercrops appeared to be due primarily to improved resource use through resource partitioning and compensatory growth, rather than resistance to pests, diseases, and other natural stressors. Improved stability in intercrops was related to both compensatory growth and the lower responsiveness expected in more productive systems.

Combining species that are complementary in resource use and have high capacity for compensatory growth should improve system productivity and stability. Combining species with differing sensitivity to various types of stressors (competition, moisture, nutrients, pests, windstorms, etc.) should further increase stability. Inclusion of one or more species that is stable and gives at least a moderate yield will assure a reliable minimum caloric yield. Other species in the system should be nutritionally complementary, either by supplying high quantity and/or

quality of protein, or by high vitamin and mineral content. Nutritional considerations are particularly important for subsistence agricultural systems.

The characteristics of component species of the four-crop system fit the above description (Table 79). Aggressive and subordinate species, and stable and unstable species, were combined with positive effects on system productivity and stability. Sorghum was a consistently stable and productive element of the system. Maize was productive, but less stable, and was responsive to changes in competition and environmental fluctuations occurring after planting. Cowpea and pumpkin were relatively low-yielding and unstable, as is likely true of most dicots in comparison with the major monocot grain crops. Pumpkin, however, was capable of surprisingly high edible yield in a good year, and both cowpea and pumpkin contributed high nutritional quality (protein, vitamins, minerals) to the system. The role of these crops, then, appears to be provision of nutritional diversity and quality, high capacity for compensatory growth, and (in the case of cowpea) suppression of weed growth in intercrop systems.

Even distribution of roots and leaves throughout their respective profiles was associated with high system productivity; improved resource use in these zones probably occurs as a result of complementary vertical stratification by species of leaves and roots. In addition, complementary light requirements of sun-adapted C-4 species placed in the upper canopy and shade tolerant C-3 species in the lower canopy may have contributed to the success of the four-crop system. Nutrient requirements of the components of the four-crop system were not investigated, but it is

Table 79. Summary of species' roles in the four-crop intercrop system.

SPECIES	PRODUCTIVITY	NUTRITIONAL QUALITY[a]	AGGRESSIVE-NESS	STABILITY WITH RESPECT TO		
				PESTS	COMPETITION	OVERALL GROWTH CONDITIONS[b]
MAIZE	High	Med	High	High	Low	Med
SORGHUM	High	Med	Med	High	High	High
COWPEA	Med-Low	High	Med	Low	Low	Low
PUMPKIN	Med-Low	Med-High	Low	Low	Low	Low

[a] protein or vitamin/mineral content

[b] from year-to-year, within-year, and treatment variability analysis

known that maize has high nitrogen requirements, while cowpea is a nitrogen fixer, an example of complementary requirements. In terms of temporal patterns of resource use, sorghum grew more rapidly than the other agronomic species, but ceased growing earlier in the season. Continuing development of pumpkin late in the growing season may have also contributed to temporal resource partitioning.

The four-crop system was most like successional vegetation in several aspects of structure and function, but the productivity advantage of the four-crop system compared with monocultures was not greater than that of the two-species intercrop systems in Year 1. Combination of monocots and dicots seems to work well as a rule; the benefit of inter-cropping was clearly lowest in the maize-sorghum system, which contained no dicots and was rather unlike the successional system in aboveground structure. In both the successional vegetation and the intercrop systems, dicots responded more strongly to defoliation than monocots, indicating their role in compensatory growth.

Successional vegetation developed a much higher LAI and canopy cover than the agronomic systems, but its productivity and stability were about equal to that of the most stable and productive crop system, sorghum monoculture. Successional vegetation stopped growing earlier in the season than the agricultural systems, so that estimates of productivity based on changes in standing crop without correction for leaf fall may underestimate NPP by a larger amount in succession than in the crop systems. High productivity during the first half of the growing season and early maturation may be adaptations to un-predictable rainfall at the end of the growing season, when moisture

levels can be critical for grain filling. The early maturation of sorghum may be one reason for its high yield stability.

Environmental Stability and Intercropping

The Morogoro environment could be characterized as having low but stable nutrient supplies and unpredictable rainfall during periods critical for crop growth. In such unstable and stressful environments, intercropping is expected to be consistently more productive and stable than corresponding monocultures due primarily to resource partitioning and compensatory growth. A monoculture of a species very well adapted to the prevailing stressors may be more productive and stable than the intercrop, however. This was the case with sorghum monoculture, which was more productive and stable than the four-crop intercrop. An intercrop composed entirely of species well adapted to the prevailing stressors (e.g., sorghum and millet, in arid areas) would perhaps be the most stable and productive system in a stressful and unstable environment.

In a very stable environment the benefits of resource partitioning would still favor intercrops in terms of yield, but the yield-stabilizing effects of compensatory growth would be reduced. In a very productive environment the benefits of both resource partitioning and compensatory growth would be reduced due to decreased competition, but would nevertheless enhance the stability of intercrops compared with monocultures.

CHAPTER EIGHT
IMPLICATIONS FOR TANZANIAN AGRICULTURE

The greater productivity, stability, and resource use efficiency of intercropping systems under farmers' conditions suggest that these systems should not be hastily replaced by monocultures. The combination of high productivity and high stability implies reduced probability that food yield will fall below a minimum level (low risk). In particular, the recommended-density maize monoculture did not perform well in comparison with equivalent density intercrops, equivalent-density sorghum monoculture, or reduced-density maize monoculture. Sorghum was both stable and productive, and increased emphasis on this crop in Tanzanian agriculture appears desirable. Cowpea and pumpkin, while rather unproductive in this study, provided dietary diversity and had high capacity for compensatory growth, contributing to system stability. The same is likely to be true for many other minor crops widely used in traditional cropping systems. The high response to fertilization, the greater yield stability in fertilized plots, and increased labor use efficiency with fertilization, all argue for increased use of fertilizer inputs where economics permit.

This study was designed as a controlled-density comparison of interplanted fields with the same crops grown separately, and did not attempt to answer other important questions related to intercropping. Several lines of further research are suggested by this study, that would aid in the development of stable and productive food production

systems for the environmentally unstable semiarid areas of Tanzania. Some unresolved problems for future research include the following:

(1) Do intercropping systems maintain a yield and stability advantage over monocultures at higher planting densities?

(2) How great is the potential for pest control through ecosystem design? What are the effects of field size, and what factors determine pest levels and stability? Resource concentration, pest dilution, pest mobility and search behavior, crop resistance and palatability, crop resilience, and natural enemy effects have all been suggested as mechanisms determining pest productivity and stability.

(3) Can staggered planting (of a given species) and staggered or relay planting of different species increase productivity and/or reduce risk? Use of computer models of rainfall predictability and crop growth requirements may be a more productive approach to this problem than extensive field trials.

(4) Is labor the factor that most strongly limits Tanzanian agricultural productivity? More detailed studies of labor use in all agricultural operations (including walking to distant fields, transporting inputs such as fertilizer, and processing) are required to determine: (a) total levels of labor input in various cropping systems, and the efficiency of their use, (b) the times of year that labor shortages are most critical, and (c) how agronomic operations and cropping systems can be modified to make maximally efficient use of the available labor supply.

CHAPTER NINE
CONCLUSIONS

In this study, effects of crop system diversity on the productivity and stability of the systems as a whole and their component species were examined. Productivity was measured by a number of measures of biomass accretion (over each of two growing seasons) as well as measures of biomass distribution. Intercrop performance was compared with that of a mixture of corresponding monocultures with a new index called Yield Equivalent Ratio (YER), the ratio of actual intercrop yield to the expected yield (based on planting densities and monoculture yields of the component crops). Stability was measured as the coefficient of variation among years and among plots, and as percent response to stress treatments. The crop systems were planted at equivalent densities, so the effects of intercropping were due only to differences in spatial diversity, and not to the degree of packing. Several types and intensities of stress (fertilization, watering, pesticide spraying, defoliation) were applied to determine the effects of stress on simple and diverse systems. The hypotheses outlined in Chapter One are restated below, and the major results summarized.

Hypothesis 1. Diverse systems are more productive than corresponding monocultures.

Finding: True for all systems studied; YERs for various productivity measures were consistently greater than one, but not always significantly so. Edible yield advantage

was greater than that by other productivity measures due to reduced root/shoot ratios and increased allocation ratios in more productive systems and treatments.

Corollary A. Intercrop productivity is intermediate between that of its most and least productive components.

<u>Finding</u>: Maize and sorghum monocultures were usually more productive than the intercrop systems by many measures; cowpea and pumpkin were usually less productive.

Corollary B. The greater the stress, the greater the intercrop productivity advantage.

<u>Finding</u>: This relationship was not quantitfiable since measures of stress were not obtained that were independent of productivity. If level of productivity is used as a measure of stress intensity, then the intercrop advantage should have been greater in the fertilized than in the control treatment by this corollary; it was approximately equal. Intercrop advantage was lowest (nearly zero) in the defoliated plots, but this may have been due to changes in canopy structure rather than to reduced productivity in general (high stress).

Hypothesis 2. Yield constancy (stability) in intercrops is greater than that of corresponding monocultures.

<u>Finding</u>: Intercrop stability was consistently slightly greater than that of corresponding monocultures from year to year and among treatments. Point-to-point stability of intercrops and corresponding monocultures could not be compared because the monocultures were not paired in the experimental design. Risk reduction in intercrops is due to both increased yield levels and increased yield stability.

Corollary A. Intercrop stability is intermediate between that of its most stable and least stable components.

<u>Finding</u>: Sorghum monoculture was consistently more stable, and cowpea and pumpkin monocultures less stable, than the intercrop systems.

Corollary B. Stability of all systems is greatest under low stress.

<u>Finding</u>: Yield stability among plots in Year 2 was greater in fertilized (low-stress) than control (higher-stress) plots.

Hypothesis 3. Some species are more productive in diverse systems than in monoculture; others are more productive in monoculture.

<u>Finding</u>: Maize and sorghum were consistently more productive in intercrops than in monocultures; cowpea was equally or more productive in intercrops, and pumpkin was less productive in intercrops than in monoculture.

Hypothesis 4. Some species are more stable in diverse systems than in monocultures; others are more stable in monoculture.

<u>Finding</u>: Maize was consistently more stable in intercrops than in monoculture, but sorghum, cowpea, and pumpkin were less stable in intercrops. Reduced stability of some or all species in an intercrop may reflect fluctuations in the competitive environment, and compensatory growth in response to those fluctuations. As such, species instability can contribute to system stability.

Hypothesis 5. Pest and disease levels are lower and pest stability higher in diverse systems than in monocultures.

<u>Finding</u>: Levels of several pests were correlated with productivity differences among plots or among years, but few pests were significantly more or less abundant in intercrops than monocultures. Pest levels are therefore not thought to be responsible for the intercrop/monoculture yield differences. Cowpea was strongly pest-limited, as indicated by its very positive response to the pesticide treatment; levels of unmeasured cowpea pests could be partly responsible for intercrop/monoculture differences in cowpea.

Hypothesis 6. Efficiency of resource use is greater in intercrops than in monocultures.

<u>Finding</u>: Overall resource use efficiency (output/total resource supply) was greater in intercrops than monocultures. Labor use efficiency in intercrops was also equal to

or greater than that in corresponding monocultures, although the amounts of labor used were usually greater in the intercrops.

Corollary A. Root and leaf systems are vertically stratified by species, and leaf and root profiles are more evenly filled in intercrops than monocultures.

<u>Finding</u>: Leaf profiles were vertically stratified by species, with sun-adapted species in the top of the canopy and shade-adapted species in the lower strata. Sorghum rooting appeared to be deeper than that of pumpkin. Root biomass was higher in the four-crop system than in the other crop systems. The leaf profile was most evenly filled in the four-crop system, but roots were not particularly evenly distributed in the four-crop intercrop.

Corollary B. Compensation occurs among components of diverse systems; low productivity by one species causes increased productivity of others.

<u>Finding</u>: Compensatory growth is difficult to measure without controlled plant-removal experiments. Negative correlations (among plots) of cowpea growth with that of maize, sorghum, and pumpkin, and of successional monocots with successional dicots, suggest compensatory growth.

Successional dicots and cowpeas appeared to compensate for loss of overstory monocots in the defoliation treatment.

Corollary C. Intercrop systems composed of species with unlike resource response curves and temporal growth patterns have the greatest productivity advantage compared with corresponding monocultures.

Finding: Intercrop advantage was lowest in the maize-sorghum system, composed of two ecologically similar species. This mixture may be more advantageous in low rainfall years, however, because of complementary moisture response. Intercrop advantage was high in the maize-cowpea system (possibly due to reduced competition for nitrogen) and in the four-crop system, which combined species of different productivities, resource response curves, temporal growth patterns, and nutritional value.

Hypothesis 7. Successional vegetation of the same age as the crop systems is the most productive and stable of all systems, and has the most evenly filled root and leaf profiles.

Finding: Successional vegetation was the most productive system studied (followed closely by sorghum monoculture). Net primary productivity of the successional system may be even greater than indicated by these results, if leaf turnover were taken into account. Succession was one of the most stable systems from year to year, but

was only intermediate in stability by a summed rank of several stability measures. Leaf Area Index, root biomass, and canopy cover were clearly higher in the successional system than in any crop system; root and leaf profiles were also filled evenly (vertically). The four-crop system was the most structurally similar to successional vegetation of the crop systems studied.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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